The senses of the insects

Auguste Forel

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THE SENSES OF INSECTS

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SENSES OF INSECTS

BY

Henri

AUGUSTE FOREL

TRANSLATED BY

MACLEOD YEARSLEY, F.R.C.S.

WITH TWO PLATES

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THIS TRANSLATION IS

DEDICATED

TO

LORD AVEBURY

WHOSE PATIENT WORK UPON THE HABITS

OF THE SOCIAL HYMENOPTERA

AND UPON THE SENSES OF INSECTS IN GENERAL

IS APPRECIATED BY ALL ENGLISH MEN OF

SCIENCE

TRANSLATOR'S PREFACE

THE translation of Dr Forel's "Senses of Insects" has been a labour of love. His work is but little known in this country, save to a few physiologists, and to those entomologists who have turned their attention to the psychology of insects. By them it is fully appreciated. The work contains, however, so many interesting experimental details, exhibits such a wide field of painstaking investigation, such sound logic, and so liberal and open-minded a treatment of the subject, that I feel sure it only requires translation to find a considerable audience in the United Kingdom.

There is a growing tendency amongst the laity to tread not only the broad highways of science, but to explore its more fascinating by-paths. This tendency cannot be too carefully fostered, for it is in the right direction, a direction which leads away from superstition and narrow-minded bigotry and towards truth. The eagerness of Dr Forel for the establishment of truth is only equalled by his contempt for those who publish opinions based upon the so-called "results" of experiments made either imperfectly and carelessly or with a scarcely concealed bias. These pseudo-scientific "investigators" he demolishes with a pitiless logic.

Even to those who do not wish to plunge headlong into the depths of scientific technicalities, Dr Forel's work will still have much interest. It will open up to them a field of observation (possibly undreamed of) in insect life; it will teach them to look with a more kindly eye upon these beings, and it cannot but widen their minds as it does their observation.

A few words as to the work of translation itself. It has been done in leisure moments and has been a source of great pleasure to me. I must gratefully acknowledge the very great help given to me by my friend Mr H. B. Grimsdale, M.B., F.R.C.S., in so kindly going through the whole MS. with me and making many alterations and suggestions. I have added certain footnotes where I have deemed it advisable to do so, and I have (with Dr Forel's permission) taken upon myself the task of questioning the assertions of Cyon and others in regard to the Japanese dancing mice.

Some rearrangement of the subject matter has been necessary, as the original is contained in five parts, published separately and at intervals of time. Of these I have placed Part I. (a free translation from *Mittheilungen des Münchener entomologischen Vereins*, 1878: Forel, *Beitr. z. Kenntn. d. Sinnesempfindungen d. Insecten*) in Chapters i. and ii.; Part II. (written in 1885) in Chapter iii., and the experiments of 1886-7 in Chapters iv. to viii. The third Part, which criticises the experiments of other observers subsequent to 1887, and describes further researches of Forel's own, will be found in Chapter ix., to which is added, as a note, the commencement of Part IV. The remainder of this Part, dealing with orientation in space, occupies Chapter x. Part V., a continuation (1901) of the same subject, I have considered as best occupying another Chapter (xi.), and with this I have incorporated Forel's latest work, on the memory of time in bees, done in 1906. The remainder of Part V. will be found in Chapter xii.

I have also to thank Dr Forel for permitting me to translate his work, Lord Avebury for his kind permission to dedicate the work to him, and my friend Dr Gray for making the preparation of which Plate II. is a photograph.

MACLEOD YEARSLEY

31 Harley Street, W.
December 18th, 1907

AUTHOR'S PREFACE

HAVING decided to republish my early experiments, encouraged thereto by the kindness of Dr Celesia, I must endeavour to justify my decision to the reader by offering him the following good reasons for this step.

Misfortune attended the publication of my experiments. The early ones appeared in German in a local journal which did not long survive its birth. The complete account of them appeared in the *Recueil Zoologique Suisse*, a journal which was both dear and of small circulation, whose life was hardly longer than that of its predecessor, and which allowed but a limited number of reprints. Several authors, who worked later at the subject, were obliged to borrow this publication from me in order to consult it.

Nevertheless the subject is one of great interest, as much from the standpoint of biology as from that of comparative psychology. The very peculiar mechanism of instincts always has its starting-point in sensory stimuli. To comprehend this mechanism it is essential to understand thoroughly the organs of sense and their special functions. It is, further, necessary to study the co-ordination which exists between the action of the different senses, and leads to their intimate connection with the functions of the nerve centres, that is to say, with the specially instinctive intelligence of insects. The whole question is, therefore, a chapter of comparative psychology, a chapter in which it is necessary to take careful note of every factor, to place oneself, so to say, on a level with the mind of an insect, and above all, to avoid the "anthropocentric" errors with which works upon the subject are filled. At the same time the other extreme must equally be avoided—"anthropophobia," which at all costs desires to see in every living organism a "machine," forgetting that a "machine" which lives, that is to say, which grows, takes in nutriment, and strikes a balance between income and expenditure, which, in a word, continually reconstructs itself, is not a "machine," but something entirely different. It is, in fact, a problem to which we have not the key, and of which we can but study the form and function without comprehending the intimate connections of their causality, which are those of protoplasmic life.

In other words, it is necessary to steer clear of two dangers. We must avoid (1) identifying the mind of an insect with our own, but above all (2) imagining that we, with what knowledge we possess, can reconstruct the mind by our chemical and physical laws. On the other hand, we have to recognise the fact that this mind and the sensory functions which put it on its guard are derived—just as with our human selves—from the primitive protoplasmic life. This life, so far as it is specialised in the nervous system by nerve irritability and its connections with the contractility of the muscular system, is manifested under two aspects. These may be likened to two branches of one trunk.

(*a*) *Automatic* or *instinctive* activity. This is acquired by repetition and is inherited through the nuclei of the conjugated ovum and spermatozoon in the form of hereditary energy or power. It is uncontrollable and constant in effect, adapted to the circumstances of the special life of the species, the genus, etc. It is this curious instinctive adaptation (which is so intelligent when it carries out its proper task, so stupid and incapable when diverted to some other purpose) that has deceived so many scientists and philosophers by its insidious analogy with humanly constructed machines.

But, automatic as it may appear, instinct is not invariable. In the first place it presents a phylogenetic evolution which of itself alone already expresses a certain degree of plasticity in the series of generations. It presents, further, individual variations which are more distinct as it is less deeply fixed by heredity. The divergent instincts of two varieties, for example, present more individual variability and adaptability than do those instincts common to all species of a genus. In short, if we carefully study the behaviour of each individual of a species of insects with a developed brain (as has been done by P. Huber, Lubbock, Wasmann, and myself, amongst others, for the social hymenoptera), we are not long in finding noteworthy differences, especially when we put the instinct under abnormal conditions. We then force the nervous activity of these insects to present a second and plastic aspect, which has been to a large extent hidden from us under their enormously developed instinct.

(*b*) The *plastic* or *adaptive* activity is by no means (as has been so often suggested) a derivative of instinct. It is primitive. It is even the fundamental condition of the evolution of life. The living being is distinguished by its power of adaptation. The amœba is plastic. But in order that one individual may adapt itself to a host of conditions and possibilities (as is the case with the higher mammals and especially with man), the "brain" requires an enormous quantity of nerve elements. But this is not the case with the fixed and specialised adaptation of instinct.

The neuro-muscular system, then, adapted to irritability[1] and movement, is the first branch derived from the primitive stem of protoplasmic life.

Later, from this primitive trunk, two varieties of central nervous activity or "*neurochyme*," as I prefer to call it, are simultaneously derived: (1) a plastic activity, by which the animal immediately reacts to all new stimuli and adapts itself to them more or less efficiently according to the number of nerve elements possessed by it capable of co-ordinating their reaction to external influences. This activity is—as a result of its autoplasticity—slower and more clumsy, but it has the invaluable advantage of opening up new paths for adaptation to the unexpected, of preparing by repetition secondary automatic activities (habits) which, by their increasing fixation, form the gradual passage from plastic to automatic activity. Further, it prepares in the germ protoplasm, in a manner at present obscure, by the hidden methods of natural selection and other factors of heredity, the determinants of hereditary dispositions and complete hereditary automatisms or instincts. I cannot enter here into the discussion of hypotheses as to the laws of heredity, preferring to keep to the domain of facts. (2) An automatic or predetermined activity, fixed by the repetition and long special adaptation of the plastic activity which has, by that very repetition, lost its plasticity. In secondary automatism, or habit, which we observe in ourselves, it is easy to study how this activity, derived from plastic activity and ever becoming more prompt, complex, and sure (technical habits), necessitates less and less expenditure of nerve effort. It is very difficult to understand how inherited instinct, hereditary automatism, could have originated from the plastic activities of our ancestors. It seems as if a very slow selection, among individuals best adapted in consequence of fortunate parentage, might perhaps account for it. But there is still so much obscurity in hereditary forces and in the causes which develop or inhibit them, that it is better to reserve judgment upon the subject.

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[1] I cannot say sensitivity, because the term sensibility is anthropocentric and refers to the conscience or inside (psychological) of the mind, which man can only judge of by comparison with his own. It is evident that there should be a form of consciousness and sensitivity corresponding to the nerve irritability of the lower animals, but we are unable to picture it.

To sum up, every animal possesses two kinds of activity in varying degree, sometimes one, sometimes the other predominating. In the lowest beings they are both rudimentary. In insects, special automatic activity reaches the summit of development and predominance; in man, on the contrary, with his great brain development, plastic activity is elevated to an extraordinary height, above all by language and before all by written language, which substitutes graphic fixation for secondary automatism, and allows the accumulation outside the brain of the knowledge of past generations, thus leaving to the last the forces necessary to his plastic activity, at once the adapter and combiner.

We shall first recapitulate our original experiments for what they are worth, and then pass on to review critically what has been done since upon the subject.

AUGUSTE FOREL

CHIGNY, *March 12th, 1900*

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Membraneous labyrinth of a Japanese Dancing Mouse (*Mus. Musculus, var.*). From a preparation by Dr Albert A. Gray.

THE SENSES OF INSECTS

CHAPTER I

GENERAL CONSIDERATIONS

LET us, at the outset, make reference to several points of importance which, as a rule, have been too much neglected.

1. When we wish to judge of the sensations of the lower animals, in the first place we do not detect any morphological homology between their senses and ours. We only find analogies which proceed from a certain homology of functions, or from adaptation towards an analogous end (convergence). This analogy of functions can only be demonstrated by experiments or observations on the living animal. It is, therefore, absurd to attempt to assume directly from accidental resemblances between the situation and shape of certain organs in vertebrates and insects that they are equivalent either phylogenetically or physiologically. By reasoning thus (the example is as amusing as it is characteristic) Paasch[1] and Wolff[2] found the olfactory organ of insects in the mid-line of the face, *because* the nose of man is so situated. Wolff (*l.c.* p. 63) calls the labium "the nasal bone," and thinks it necessary to note the absence of the intermaxillary bone in insects!

2. Physiological deductions drawn from analogies of the same kind have no more value. When, for example, it is said (Wolff, Paasch, etc.) that a damp mucous membrane is necessary to olfaction, it is absolutely unproven. We merely know that the olfactory organ of vertebrates is situated in a damp mucous membrane and no more; we do not know upon what the olfactory sense itself depends. Similarly, we are not

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[1] *Troschel's Archiv für Naturgeschichte*, 1873, Bd. i. p. 248.

[2] *Das Riechorgan der Biene.* Nova Acta der K. L. Car. Deutschen Akad. der Naturforscher, Bd. xxxviii. Nr. 1, 1875.

authorised to assume that a stretched membrane is necessary to hearing.

3. When we judge of the sensations of animals, we must assume nothing of their quality, properly so-called. This is especially true for the invertebrates, whose senses present scarcely any morphological homology with our own. In the case of the eye, the absence or presence of certain optic apparatus may allow us to conclude more or less as to the formation or non-formation, size, situation, and distinctness of an image; but we know nothing of *how* this image is perceived by the nervous system. We can, as a set-off, conjecture the manner in which the animal reacts relatively to certain stimuli, and conclude from our observations that such an organ has the property of making the animal perceive in some fashion such a physical or chemical phenomenon, the presence of such an object, or of such a substance. And here we are ourselves dependent upon our own senses, and can only judge of minute details when we ourselves are capable of perceiving those details, which is especially the case for visual sensations. We can thus show by experiment if, by the aid of such and such an organ, an animal is able to distinguish light, colour, movement, or form of objects, whether it can distinguish them at a distance or only near, clearly or only indistinctly, etc. In the case of hearing, it is at present practically impossible for us to judge what differences the animal perceives in the qualities of sound waves. In the case of smell we can only say: such an organ gives the animal knowledge of such a substance, of such a being, of such an object, without the intervention of sound, light, or the mechanical vibration of intermediate media, across this medium, at such and such a distance, under certain circumstances. We can only judge of the animal's sense of smell by the reactions which occur when it runs away from or searches for what it has just perceived. It is impossible to give any other definition of smell or of its organ in the lower animals; all that we know further is hypothetical. In the case of the sense of touch and its varieties, we are, equally, only able to judge of the reactions of the animal following upon immediate contact, mechanical vibrations, movements of the air, the action of corrosive substances, the action of temperature, etc. We can

only judge of pain by probable analogy (reactions of the animal more or less analogous to our own); here we are absolutely without an objective criterion, the sensation of pain only differs from that of touch by subjective qualities. When an animal can distinguish different qualities of food one from another, by contact with the mouth, and is unable to distinguish them at a distance or by touch, we may speak of a sense of taste, although we have, nevertheless, not demonstrated it clearly.

The imperfect nature of these definitions stares us in the face. It is therefore very possible, as Leydig in particular has often suggested, that certain animals possess a sixth, or a seventh, sense, without our being able to prove it; that is to say, that they have a subjective sensation of a particular quality for a certain group of adequate stimuli which we cannot either perceive, or cannot distinguish from other sensations.

It is thus that insects, apart from sight and hearing, may be able to perceive distant objects in two or three ways subjectively distinct by means of different nerve terminations, corresponding to efficient physical and chemical stimulating agents which are perhaps known to us, perhaps yet unknown. We are obliged to refer all such matters to the sense of smell, knowing no better, and only able to represent other sensations by our own.

4. Certain careful and judicious observers, like Dugès,[1] Perris,[2] and Graber[3] have paid attention to two capital errors in the method of experimenting, errors which we see constantly repeated with inconceivable blindness. First it is impossible to draw conclusions as to the sense of smell in invertebrates from the effect produced upon them by chemical substances of which the fumes have a powerful action, such as ammonia, chloroform, turpentine, etc., because these fumes irritate the tactile nerve terminations directly and probably painfully, as they do in those of our own conjunctivæ. It is necessary, on the contrary, to employ substances which serve as food to the animal in question, or to its young, especially the substances which it is in

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[1] Ant. Dugès, *Traité de physiologie comparée de l'homme et des animaux.* Montpellier et Paris, 1838.

[2] Ed. Perris, *Mémoire sur le siège de l'odorat dans les articulés.* Extr. des Actes de la Société Linnéenne de Bordeaux, t. xvi. liv. 3 et 4, 1850.

[3] Graber, *Die tympanalen Sinnesapparate der Orthopteren.* Denkschriften der K. K. Akad. Wissenschaften in Wien, Bd. xxxvi.

the habit of seeking or avoiding in the natural state, since the same are often odourless to us. Our subjective measure here is of no value. Whoever thought of measuring the delicacy of a dog's sense of smell with camphor or turpentine? And yet the dog is our far nearer relative than the insect!

Secondly, we should not confuse the disturbance of the tactile nerves with hearing, as Léon Dufour,[1] Paasch (*l.c.*), Landois,[2] and others have constantly done, and as Lubbock himself has done once.[3] To avoid this it is necessary to experiment with special care, and I cannot sufficiently recommend as a guide the study of the intelligible and precise experiments of Graber (*l.c.* to the end).[4]

5. When experiment has proved that an organ is the seat of a sense, the anatomical demonstration of a terminal nerve apparatus therein is a very necessary confirmation of the experiment. A negative result is a reason for doubting the accuracy of the latter. But one should be on guard against exaggerating the import of positive results, and especially against inferring function from anatomical structure. There are so many terminal nerve organs in the bodies of insects, and they are so varied, both in their situation and structure, that one is always at a loss to find work for them. It will be

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[1] Léon Dufour, *Quelques mots sur l'organe de l'odorat et sur celui de l'ouïe dans les insectes.* Actes de la Société Linn. de Bordeaux, t. xvi. liv. 3 et 4, 1850.

[2] H. Landois, *Thierstimmen.* Freiburg i. B., 1874, pp. 124-134. Landois (Arch. iv. f. microsc. Anat. v. Schulze, Bd. iv. p. 88) has also fallen into the first of the errors of which we speak.

[3] Lubbock, *On some Points in the Anatomy of Ants.* The Monthly Microsopical Journal, Sept. 1877, pp. 132-133. Lubbock here quotes some of my own observations (*Fourmis de la Suisse*, p. 121) from which he believes, contrary to my opinion, that ants hear. But all my observations are well explained, in my opinion, some by the sight of movements, the others by the vibration of the underlying base. I might reply to Lubbock that these are much more in accord with his own observations (Linnean Soc. Journal, vol. xii. *Observations on Bees and Wasps*), in which all the noise he made was noted neither by the bees nor by the wasps, which speaks against his actual opinion (1878).

(P.S. 1885. The remarkable experiments made and published since by Lubbock are all in support of my opinion. He himself tried, in different ways, the production of sounds imperceptible to us by their very great number of vibrations; the results have always been negative. No one of the different hymenoptera has appeared to perceive them in the least.)

[4] P.S. 1885. It is inconceivable how Graber can have abandoned the ground of his own experiments to admit, without control, the impossible theories of Wolff.

granted that we have a right to assume that a certain terminal organ, if it is really the seat of a sense, ought to be large in insects which have this sense well developed and vice versâ. This is, however, one of the matters which receive least attention.

The most constant and important terminal apparatus in insects consist of (1) the faceted eyes, (2) the antennæ. Each of these organs receives a relatively enormous nerve, and to each of these nerves corresponds a special lobe of the brain (subœsophageal ganglion). No other nerve exhibits any similar arrangement. One finds further sensory nerve terminations (3) in the ocelli, (4) in the palpi, (5) in various parts of the mouth (tongue, jaws, pharynx). They are also sometimes found in the tarsi, at the base of the wings, on the sides of the body, in the anterior tibiæ, etc.

6. According to the families, genera, and species of insects the development of different senses varies extremely. We meet with most striking contrasts, and contrasts which have not been sufficiently noticed. Certain insects (dragon-flies, for instance) live almost entirely by means of sight. Others are blind or almost blind, and subsist exclusively by smell and taste (insects inhabiting caves, most working ants). Hearing is well developed in certain forms (crickets, locusts), but most insects appear not to hear, or to hear with difficulty. Despite their thick chitinous skeleton, almost all insects have extremely sensitive touch, especially in the antennæ, but not confined thereto ; most of them certainly also possess the sense of taste.

It is absolutely necessary to bear in mind the mental faculties of insects in order to judge with a fair degree of accuracy how they use their senses. We shall return to that point at the end of this work.

The publications which have appeared upon the subject before us are very numerous, but they consist for the most part of theoretical dissertations only, of hypothesis, and, as Lubbock (*l.c. Obs. on Bees, etc.*) has very well remarked, of oft-told tales of ancient experiments, borrowed, through more than a century, from one "authority" by another, without attempt at control or checking. The observations which follow are, therefore, not superfluous.

CHAPTER II

VISION

IN vision we are dealing with a certain definite stimulus—light, with its two modifications, colour and motion. Insects have two sense organs for vision, the faceted eye and the so-called simple eye, or *ocellus*. A few words as to the important researches that have been made with regard to these organs will not be out of place.

Grenacher[1] has definitely proved that the faceted eyes and the ocelli are derived from one and the same organ, the former by the multiplication, the latter by the simple augmentation of the number of their histological elements.[2] He has shown further that the compound eyes of various insects are of a very different structure one from another, and can be traced back to the ocellus by all kinds of intermediate forms. It was at one time thought that each facet of the compound eye had a conical crystalline lens and a central visual rod (rhabdoma) in the centre of its retinule. Grenacher has proved that this is by no means the case. In the heteropterous Hemiptera, the Nemocera, and the lower Coleoptera, there is no crystalline; further, each cell of the retinule has, as in the ocelli, its own rod. In spite of the absence of the crystalline, its four hypodermic cells (*Matrixzellen*) exist in each facet; they are homologous with what are called the "cells of the vitreous body" of an ocellus. The retinule of each facet of this incomplete compound eye which Grenacher has called the *acone eye* exactly corresponds with the retina of the ocellus. Finally, Grenacher has shown that the so-called cells of the vitreous body, of the crystalline, and the peripheral portion (rod) of the retinal cells are only modified hypodermic cells of the chitinous skin, invaginated and separated by constriction, just as the cornea itself is only the modified chitinous skin (external cuticle). In the eye with the ordinary crystalline (*eucone eye* of Grenacher), the pigment which isolates each facet (each crystalline) one from the other affords only an opening of extreme minuteness at the posterior extremity of each crystalline to allow of the passage of the pencil of luminous rays, and the retinule of each facet consists of a very limited number of cells only (four to eight). The rods of the anterior extremity of these cells are welded together, forming a single large rhabdome, whilst their posterior ends extend into the fibres of the optic nerve or lobe.

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[1] Grenacher, *Zur Morphol. u. Physiol. des facett. Arthropo. Auges.* Nachr. v. d. K. Gesellsch. d. Wissensch. a. d. G. A. Univ. zu Göttingen, Nr. 26, 23. Dezember 1874. Grenacher, *Untersuch. über das Arthropodenauge im Auszuge mitgetheilt.* Beilageheft z. d. Klin. Monatsblättern für Augenheilkunde, Mai-Heft, xv. Jahrgang, Rostock, 1877.

[2] Grenacher has remarked that the ocelli have not always a different morphological seat from that of the compound eyes; the flea, for example, has ocelli instead of and in the situation of faceted eyes. I may add that the same thing occurs in the genus of American ants *Eciton*. The workers of this genus have instead of and in the situation of compound eyes a large spherical ocellus on each side. They have not, on the contrary, any ocelli on the forehead. The allied forms of these curious ants are some blind, others with ordinary compound eyes (see Fig. 5).

These facts make the projection of a tiny reversed image of an object upon the retinule impossible, even if the cornea always produced one.[1] And even if such an image could be projected, would the several elements of the retinule suffice to receive and transmit it to the brain?

This physiological problem has been solved in the most remarkable fashion by the physiologist Exner,[2] independently of Grenacher. The entire agreement of the results of the work of these two authors, from completely different points of view, is the best proof of their truth. Exner proves that the image formed by the cornea of the facets is destroyed by the crystalline, and that all this apparatus only serves to concentrate as much light as possible upon one point, *i.e.* on the posterior pole of the crystalline, by the multiple reflection of the light rays. Exner calculates the refraction, the focus, etc., of the cornea of a facet of *Hydrophilus*, and shows that even if an image could be formed through the crystalline (which is not the case), this image would be formed well behind the retinule. By experiment he shows that the optical sensation of motion is something distinct from that of colour, even in the human eye, where it has a special place in the lateral periphery of the retinal field, completely independent of the distinct perception of objects. The faceted eye, which does not project the image upon one point of the retina, but which receives upon its numerous retinules light on many different points, will nevertheless perceive every movement of an object in a great number of facets by means of the increase, diminution, and change of quality of the light in each of them. This form of eye, therefore, ought to be very appropriate for perceiving motion, considering the great number of elements in which the condition of stimulation is modified at the same moment by the motion of an object which comes within the field of vision. Finally, Oscar Schmidt,[1] without knowing the work of Grenacher and Exner, has recently made an observation upon certain Arthropod eyes demonstrating the impossibility of the formation of an image upon the retinule through the conical crystalline.

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[1] Grenacher has pointed out that the Hyperida which have flat corneæ which do not form any image, see very well notwithstanding.

[2] Dr Sigmund Exner, *Ueber das Sehen von Bewegungen und die Theorie des zusammengesetzten Auges*. Aus dem lxxii. Bde. der Sitzb. des K. Akad. der Wissensch., iii. Abth., Juli-Heft, 1875.

Exner and Grenacher, therefore, are both compelled to revert to the old theory of mosaic sight of Johannes Müller:[2] it is not each facet which perceives an image as Gottsche[3] thought he had demonstrated, but the insect sees a single image, more or less distinct, of the object in the form of mosaic by the fact that each facet receives a different part of the light rays given out by the object (the rays of another part of the object going to a neighbouring facet). This is comprehensible if it be remembered that the retinule at the bottom of each facet is placed, as it were, at the bottom of a tube with pigmented walls; the transparent media (*i.e.* crystalline and vitreous body) being unable to project an image, they can only concentrate the rays which fall upon the visual field of the facet.

Inasmuch as definition of the image, *i.e.* localisation of the luminous rays, depends on the co-ordination of the actions of the facets, it necessarily follows, as Müller has already pointed out, that the degree of definition varies with the number of facets. Further, the smaller the facet and the longer the crystalline, the fewer rays will the retinule perceive, but the smaller (better localised) will be the portion of the outer world from whence come the rays seen by one facet. On the other hand, the greater the facet and the shorter the crystalline, the more rays will the retinule receive, and the more intensely will they be perceived, extended, and diffused; that is to say, the less clear and more dazzling will be the sight. Therefore, many small facets diminish the intensity of the light, but augment the faculty of localisation; that is to say, the acuity of vision. When, further, the whole eye is not flat, but markedly convex, it can receive light from points so much the more widespread. This adds to the common visual field, and it appears to me that, in addition, in this case, fewer facets will simultaneously perceive rays from the same point of an object. This latter fact will tend to separate with greater definition the visual field of each facet from that of the others, which appears to me should make the perception of objects more distinct, if the number of facets is sufficiently large. Max Schulze[1] remarked (Exner) that nocturnal lepidoptera have larger facets than the diurnal, which agrees with what we have just said. In order to exercise the function of sight, the facet needs a greater pencil of light rays by night than by day. To obtain the same result we dilate our pupil. Nocturnal insects are dazzled by the light of day; diurnal insects cannot see by night. Neither the one nor the other possess the faculty of accommodation.

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[1] Oscar Schmidt, *Vortrag der Section für Zoologie* in der 50. Versammlung deutscher Naturforscher und Aertze zu München, 1877.

[2] J. Müller, *Zur vergleichenden Physiologie des Gesichtssinnes.* Leipsig, 1826.

[3] Gottsche, Müllers Archiv, 1852.

If all that we have said be true, we ought to be able to prove by observation that insects which have a number of small facets and markedly convex compound eyes are the ones that can see best, because they, in general, have the longest crystallines. Now I can prove this by my own observations, and prove further that insects are especially able to perceive motion. There are only a very few insects that can see distinctly.

For example, I watched one day a wasp (*Vespa germanica*) chasing a fly on the wall of a verandah, as is the habit of this insect at the end of summer and in the autumn. She dashed violently in flight at the flies sitting on the wall (*Musca domestica* and *Stomoxys calcitrans*), which mostly escaped. She continued her pursuit with remarkable pertinacity and succeeded on several occasions in catching a fly, which she killed, mutilated, and bore away to her nest. Each time she quickly returned to continue the hunt. In one spot of the wall was stuck a black nail, which was just the size of a fly, and I saw the wasp very frequently deceived by this nail, upon which she sprang, leaving it as soon as she perceived her error on touching it. Nevertheless she made the same mistake with the nail shortly after. I have often made similar observations. We may certainly conclude that the wasp saw something the size of a fly, but without distinguishing the details; therefore she saw it indistinctly. Evidently a wasp does not only perceive motion, she also distinguishes the size of objects. When I put dead flies on a table to be carried off by another wasp, she took them, one after another, as well as spiders and other insects of but little different size placed by their side. On the other hand, she took no notice of insects much larger or much smaller put among the flies. The last experiment is a very easy one to try for the deception of wasps by given them inert objects of the size and colour of flies.

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[1] *Die Zusammengesetzten Augen der Krebse und Insecten.* Bonn, 1868.

Most entomologists have observed with what ingenuity and sureness dragon-flies distinguish, follow, and catch the smallest insects on the wing. Of all insects they have, beyond compare, the best sight. Their enormous convex eyes have the greatest number of facets, equalled only by the eyes of the diurnal lepidoptera.[1] Their number has been estimated at 12,000, 17,000, etc. Their aerial chases resemble those of the swallows. By trying to catch them at the edge of a large pond, one can easily convince oneself that the dragon-flies amuse themselves by making sport of the hunter; they will always allow one to approach just near enough to miss catching them (I speak of *Æschna*, *Gomphus*, and *Libellula*). It can be seen to what degree they are able to measure the distance and reach of their enemy. It is an absolute fact that dragon-flies (unless it is cold or in the evening) always manage to fly at just that distance at which the entomologist cannot touch them, and they see perfectly well whether one is armed with a net or has nothing but his hands; one might even say that they measure the length of the handle of the net, for the possession of a long handle is no advantage. They fly just out of reach of one's instrument, whatever trouble one may give oneself by hiding it from them and suddenly lunging as they fly off. As regards the perception of distance, I may be permitted to point out that light issuing from a point will reach a greater number of retinules (of facets) the further this point is removed from the insect, which should make the view of the object more diffuse as the object is further removed, as Johannes Müller (*l.c.* p. 378) has already said, seeing that one facet will be reached by the light from a greater number of different points. *It is probable that this peculiarity enables the insect to measure the distance, and that the more distinctly as the insect is nearer* (*the angles varying more.*) Whoever watches butterflies and flies will soon see that these insects also can measure the distance of such objects as are not far from them.

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[1] *Vide* Meyer-Dür in *Mittheilungen der schweizerischen entomologischen Gesellschaft*, vol. iv. No. 6, 1874, pp. 320 and 337. The author describes the habits of dragon-flies and their good sight with much truth and a profound knowledge of facts. I can only concur in what he has described by my own experience.

1885. *Note.*—It appears to me that we can thus explain efficiently and satisfactorily the means whereby insects can take account of the distance of objects which are not too far away. The distinctness of the image should be increased in a regular progression in proportion as the distance diminishes. The quality of the cerebral stimulus transmitted by the visual images varies, therefore, in a regular manner (from the point of view of the degree of distinctness) according to the distance. This variation is more appreciable as the distance is shorter, and becomes by degrees *nil* or very little for long distances. Now it is known that it is the regular modifications of sensory stimuli, due to corresponding regular modifications of external agents, which allows the brain to judge of the latter, according to the habit acquired by the individual or the instinct acquired by the heredity of generations (in both cases after the repetition of adequate stimuli).

For a given insect the contours of objects ought to have a certain degree of distinctness at the distance of a metre, a certain—much greater—distinctness at a decimetre, in which case the rays proceeding from each point of the object come into the visual fields of a smaller number of facets, while the entire object will cover the visual field of a larger number of facets. Distance widens the visual field of each facet, while it confuses it with those of its neighbour. Owing to this difference, a given insect would be able to judge if an object is at one metre, at half a metre, or at a decimetre, etc. The same should hold good for the perception of motion, as Exner strongly urges. A more trifling change of position of an object placed in the visual field will suffice to set up modifications in the condition of the retinules when the object is closer, because the rays given out by the different parts of the object to different facets form greater angles between them as the distance between the object and the eye becomes shorter. The insect will therefore perceive motion less well in objects more remote. To sum up, it may be admitted that insects are all more or less short-sighted in some degree, so that the further off an object becomes, the more hazy it will be to them and vice versâ. Further, their sight ought to be not only more distinct, but at the same time their relatively distinct sight *rather longer*: (1) as the number of facets is more considerable, (2) as the crystallines are longer and the eye more convex: that follows what we have seen above. It is clear that the question is not one of myopia in the sense of human myopia, but of a relative degree of distinctness which has its maximum close to the eye. In man and vertebrates there is a certain analogy in the sense that objects as they get further away occupy a smaller and smaller place in the visual field, and consequently affect fewer and fewer of the retinal elements, making the sight less and less distinct. But the faculty of accommodation, by varying distinct sight to different distances at will, prevents us from learning to use the fact in question for the appreciation of distance. Finally, the faceted eye should be able to take better note—certainly up to a certain distance—of large than small objects, the former affecting a greater number of facets than the latter. This is a fact which I have frequently verified in ants. Small objects, especially when moving, are only perceived by them at a slight distance, because the facet in whose axis such an object is projected receives additional rays from too many other surrounding objects some way off.

The facts, as far as one can judge by the observation of the habits of insects, appear to me to point clearly to this form of vision. Insects which have large, convex eyes, with many facets, evidently see not only very clearly, but much farther than those with small, flat eyes. Every insect-hunter will agree, for example, that dragon-flies and diurnal lepidoptera see him at a much greater distance off than coleoptera and hymenoptera in general.

The males and females of bees[1] and ants distinguish one another on the wing. It is rare for an individual to lose sight of the swarm or to miss what it pursues flying. I shall show presently that the sense of smell has nothing to do with this matter.

In all these observations it is easy to see that insects, without possessing any power of accommodation, are able to perceive objects at different distances. This further corroborates the theory of Müller as well as the results obtained by Grenacher and Exner.

I have long been convinced that insects which have few facets to their eyes see very indistinctly, and I have already made this statement with regard to ants.[2] I dropped a large handful of *Lasius fuliginosus* (wood ants, used to shade) suddenly in the centre of a path under a bright sun. I squatted down at a little distance. By no concerted action, and although the midday sun threw no shadow, all the ants immediately made towards me with elevated antennæ (as if I had magnetised them). I drew back; they followed me. I then squatted down on the other side of the crowd; they at once returned and made for me again. Again I changed my position, two or three times; they always followed me. Then I quietly withdrew, following the path; they continued to follow me in a straight line, in column, without hesitating, a distance of nearly five metres, again without concerted action. But when I came to direct my steps towards a neighbouring thicket, which I nearly approached, once arrived at its edge they ceased to follow me and entered it. I then understood that the ants had mistaken me for a tree, or something similar, which they endeavoured to reach to avoid the sun. The ants of this genus did not perceive small objects, unless they chanced to be in motion and very close to their eyes. One knows, however, that the habits of insects, especially of ants, which have only two or three facets to their eyes, closely resemble those of completely blind insects (*Ponera contracta*, for instance).

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[1] The word "bee" throughout this work refers to the honey-bee, or hive-bee (*Apis mellifica*), the French *abeille*.—Trans.

[2] A. Forel, *Les fourmis de la Suisse*. Nouveaux mémoires de la Société helvétique des sciences naturelles, vol. xxvi., 1874, pp. 118, 120, 121.

With ants, as I have shown (*l.c.*), the males possess the greatest number of facets and also have the most convex eyes. They must be able to perceive the females and chase them flying. The latter, which only spend a short time in the air and play a merely passive part, have very few facets and very flat eyes. The workers, which are wingless and always live on the earth, or often even spend most of their time underground, have very flat eyes, poor in facets. This fact again agrees with anatomical and physiological results. But it must not be forgotten that, everything else being equal, the number of histological elements depends on the absolute size of the body. Thus, while the number of elements of a facet could scarcely vary in the "eucone" eye (the crystalline has always four cells), it is the number of facets which should increase with the size of the insect. Therefore the number of facets increases with two factors: the acuity of vision and the size of the insect. Let us glance at the following table, for which I have counted the facets as well as I could:—

	Formica pratensis.			Solenopsis fugax.			Aphaenogaster barbara.	
	Large Worker.	Female.	Male.	Worker.	Female.	Male.	Small Worker.	Large Worker.
Length of body	9 mill.	10 mill.	10 mill.	2 mill.	6.5 mill.	4.2 mill.	4 mill.	12 mill.
Number of facets	600	830	1200	6 to 9	200	400	90	230

A few words must be added for the perfect understanding of these figures. The small and large workers of *A. barbara* alike leave the nest and work equally in the light, whereas the worker of *Solenopsis fugax* lives almost entirely underground. The male of *S. fugax*, which is occasionally obliged to seek his female very high in the air, has only about 400 facets, considerably less than the large worker of *F. pratensis*, which has no wings but is much larger. Nevertheless, one would hardly understand this proportion if one did not know that the eye of the male of *S. fugax* is hemispherical, whilst that of the worker of *F. pratensis* is nearly flat, since the latter ant is one of the kinds of worker having the best sight, going out a great deal and climbing trees.

It can be seen how workers of ants shut up in glass receptacles, especially those of the genus *Formica*, see through the glass every movement made and reply to them by taking up a fighting position, *i.e.* erecting themselves on their hind-legs, bending round the abdomen, and opening the mandibles. They notice immobile objects much less, but they are able to perceive them, as we have seen above (*Lasius fuliginosus*). I have many times observed that the worker ants which see relatively best (*F. rufa* and *pratensis*) continually pass by the side of their larvæ and cocoons, scattered about them, without seeing them, although they were situated within their visual field and they sought them with great patience. A slight movement of the object made them see it; that is to say, they saw a movement which attracted their attention, and they recognised the cocoon at once with their antennæ. They cannot, on the contrary, perceive the tiny parasitic flies which often pursue them, nor the tiny ants of other species; they worry themselves fruitlessly and bite the air, so long as they are unable to feel them with their antennæ.

When one attentively watches a little jumping spider chasing flies on a window, one is astonished to see how bad her sight is; she can only see her prey when it walks quietly before her at about two or three inches distance, and looks for it in the wrong direction when it gets a little further away. And when the fly keeps still, this little spider, which possesses ocelli only, will yet pass even much closer to it without seeing it. If flies were not so stupid and imprudent, they would never be caught. There is a certain spider which runs along the ground and which carries her cocoon on her back. When one takes this big white bag full of eggs carefully away and puts it two or three inches from her, she forthwith starts looking for it everywhere and gives herself considerable trouble before she finds it. Johannes Müller (*l.c.*) believes that the ocelli serve for the sight of very near objects, which seems plausible. I can say nothing positive on the matter, for when it comes to a question of great proximity other senses come into play and are very easily confounded with sight. Dugés (*l.c.*) finds, like Réaumer and Marcel de Serres,[1] that in insects which have both ocelli and compound eyes the loss of the former has no effect, whilst that of the second has grave consequences for the insect. I can only confirm this opinion. As far as I can judge, wasps, humble-bees, ants, etc., find their way in the air, as on the ground, as well after the extirpation or varnishing of the ocelli as before.

It is quite otherwise when the compound eyes of flying insects are varnished or extirpated.

October 2nd, 1877, was a hot day; and there were plenty of diptera flying in the sun, among others *Calliphora vomitoria*, *Lucilia caesar*, and one other of the *Muscidae*. I completely varnished some of their eyes with an opaque varnish, and then cut off their front feet to prevent them from wiping it off. The effect of this experiment (which was often repeated) was always the same. The flies, placed on the ground, no longer flew away. Thrown in the air, they flew rapidly first in one direction, then in another, to one side or downwards, ending by dashing themselves to the ground or against the wall of a neighbouring house. The wall, like the ground, was so unforeseen by them that the force of their impact never allowed them to alight; they were always thrown back by the shock or fell to the ground,[2] where they lay quiet or beat with their wings for a moment, or started to walk again. When walking about the ground, they behaved like normal flies, but their gait was a little more slow and hesitating. Nevertheless when I picked up one of these flies several times and threw it into the air (after examining it, and, if needful, revarnishing its eyes), usually something fresh occurred, sometimes as soon as the third, but often only after the fourth, fifth, or even tenth repetition of the experiment. The fly which, the first time it was thrown, had always dashed itself to the ground or against the wall, now began, after first flying in rapid zigzags, to go directly upwards, keeping the same direction, either flying quite straight, or with a spiral rotation, now obliquely, now vertically, towards the sky. Although I have very good eyes, I always ended by losing sight of them. I was able, nevertheless, to follow with the eye to a considerable height the large *Calliphora vomitoria*, which are particularly suitable for this experiment. I obtained a similar result by the same method with the moth *Noctua gamma* and with a humble-bee. Both, after being dashed to the earth several times, ended by flying to the blue sky and disappearing. When these insects can see, they never fly skywards, where they would too soon become the prey of birds; they fly horizontally between the trees, walls, etc. Their artificially produced blindness alone explains their singular progress: thrown into the air, they are instinctively compelled to fly, but seeing nothing, they fly on until they dash themselves against some object; when they fly upwards they meet with no object.

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[1] Marcel de Serres, *Mémoire sur les yeux composés et les yeux lisses des insectes.* Montpellier, 1813.

[2] This experiment makes it at once clear that all flies which fly rapidly towards a wall or elsewhere and adroitly alight, without hitting themselves against it, must not only see, but still more necessarily be able to measure the distances very accurately by the help of their faceted eyes.

In the spring of 1878, I repeated these experiments with a like result on cockchafers. It is much more easy to follow these big insects in the air, as they fly slow. In some I removed both antennæ. They flew from the tips of my fingers like normal individuals, and quickly reached the foliage of a tree, where they alighted. I could observe nothing abnormal in their flight. I varnished the eyes of others. These flew off as quickly as the first. But, once in the air, they were incapable of directing themselves and sometimes flew downwards so as to be dashed soon to the ground and fall, sometimes upwards in a spiral, like the flies with varnished eyes, but so slowly that I was able to follow every turn of the spiral. Then, in time, they began again to fly irregularly, most often in such a way that they returned more or less to the point of departure.[1] Often, too, they hit against the wall of the house, and they generally ended by falling to the ground, but often only after several minutes. One only of these cockchafers by accident reached the foliage of a tree; he several times hit the branches and the leaves, but was unable to alight, and ended by emerging, still flying, from the opposite side of the tree. When I removed the varnish from the eyes of my cockchafers, they began to fly in whatever direction they wished and alighted upon the foliage of the trees.

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[1] Being myself lost in the country after leaving a village, in an absolutely black night, in pouring rain, I walked at random and found myself at the end of an hour at the village from which I had set out.

I also varnished the eyes of several aquatic hemiptera (*Hydrometra lacustris*). These insects, everyone knows, row with their feet on the surface of the water and are as timid as they are agile. They became incapable of perceiving my approach. Whilst they could move on the water with as much agility as before, they only started to row when I touched them, whilst their unblinded friends bolted at sight of me before I could reach the edge of the pond.

The wasps and humble-bees whose eyes were varnished or removed much more rarely flew high like the diptera. They almost always dashed against some neighbouring object, or fell. The gait of all these insects, thus blinded, on the ground is seen to be very different to their flight. Their movements are slower, more measured, but they find their way more or less well by the help of their antennæ, their palpi, or their tarsi, according as the senses of these organs are more or less developed. They then search spontaneously for a hole in which to hide (as they often do at night). Flies, wasps, etc., blinded by the method mentioned above and afterwards set at liberty in my room no longer flew towards the window, as they did when they could see, but against the wall or floor. This proves that they were no longer able to see the light. It must be made clear that I speak only of my successful experiments. If a corner of the eye remained unvarnished, the insects could still see a little and could then direct themselves more or less incompletely.

A genus of American ants, *Eciton* (Army ant, Driver ant, Tauoca), supplies us with an interesting fact. The species of this genus lead a nomadic life, are carnivorous, and hunt in great armies insects of all kinds, other ants, etc. As we have said, most of *Eciton* have two ocelli in place of compound eyes;

but several species are blind. Whilst the former (*E. hamatum*, etc.) hunt by day, in the open air, the blind species *E. Cæcum*, Latr. (= *vastator*, Smith) always hunt, according to Bates,[1] in covered galleries which they build with incredible rapidity across the roads and glades, until they reach some rotten trunk, etc., in the cavities and crevices of which they find their prey.

Insects which have very large eyes and which are essentially aerial (*Libellula*, *Tabanus*, *Bombylius*, diurnal lepidoptera, etc.), generally have the antennæ very little developed and are quite stupid in the dark. They scarcely dare to go out at night.

In other insects, as worker ants, the eyes play a subordinate part. These are the insects that may be called *Smellers* and *Tasters* (see below, extirpation of the antennæ). These latter insects work underground and by darkest night as well as by day, as I have frequently observed.

It is known that many insects will blindly fly and dash against a lamp at night, until they burn themselves. It has often been wrongly thought that they were fascinated. We ought first to remember that natural lights, concentrated at one point like our artificial lights, are extremely rare in nature. The light of day, which is the light of wild animals, is not concentrated at one point. Insects, when they are in darkness (underground, beneath bark, or leaves) are accustomed to reach the open air, where the light is everywhere diffused, by directing themselves towards the luminous point. At night, when they fly towards a lamp, they are evidently deceived and their small brains cannot comprehend the novelty of this light concentrated at one spot. Consequently their fruitless efforts are again and again renewed against the flame and the poor innocents end by burning themselves. Several domestic insects, which have evidently become little by little adapted to artificial light in the course of generations, no longer allow themselves to be deceived thereby. This is the case with house-flies (*Musca domestica*).

Cave-dwelling insects are blind. Blind arthropods, for example, a blind variety of *Gammarus puteanus*, Koch, found in subterranean waters and in the great depths of lakes, where light penetrates but feebly.[1] Exclusively subterranean animals, such as certain worker ants, moles, etc., are blind or nearly so. We thus see the number of facets of the compound eyes of worker ants of subterranean species fall to 30, to 6, to 4, to 1, and finally to 0 (*Leptanilla Revelierii*, Emery, genus *Aerictus*, and others).

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[1] Bates, *The Naturalist on the Amazons*. I have been able to confirm these facts myself recently in Columbia, in the virgin forest (1900).

By experiments as ingenious as patient, Lubbock (*l.c. Obs. on Bees, etc.*) has shown the faculty of distinguishing colours in bees and wasps. He took, for example, equal sized discs coloured red, yellow, green, and blue, placed honey on a red disc and put upon it a bee which he had marked with oil-colour. The bee flew to her hive after having eaten, but returned each time she had emptied her crop and always returned to the red disc. Then Lubbock, during her absence, substituted for the red disc a blue disc covered with honey and placed by its side another red disc identical with the first, but without the honey. The bee always went to the red disc, where she found nothing and was quite unable to find the honey on the blue disc which was at its side. This fact exhibits at the same time the inferior sense of smell possessed by bees. The experiments of Lubbock, varied and repeated in a hundred similar ways, have shown that bees distinguish all colours and seldom confound any but blue and green, whilst wasps scarcely react to differences of colour, but note better the shape of an object and the place where the honey is, so that the change of colours hardly upsets them. Further, wasps have a better sense of smell than bees.

The experiments of Plateau[2] appear to contradict these remarkable results. Plateau sought to deceive insects (bees, lepidoptera, etc.) by means of extremely well-made artificial flowers, but without any great success. The insects almost always flew to one side of these *objets d'art* without paying them any attention. Without mentioning the slight value of all negative results, there are several elements which make the experiment incomplete. Before all, it is necessary to recognise that, however exact the imitation appears to our eyes, it is possible (and also probable) that the tints and shapes may be distinguished by the eyes of the insect in a qualitatively different manner to ours, so that it perceives difference where we perceive none and vice versâ. Further, it takes no account of smell, but we see that the sense of smell does not sensibly influence the result of these experiments. Finally, the experiments of Lubbock go to show how strongly bees and wasps cling to ways and places which they know, so new flowers appearing suddenly are less likely to attract them than the old groups with which they are familiar.

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[1] 1885. I had written "never penetrates." Now it is known, thanks to M. Fol (Communication made to the Swiss Society of Natnral Science at Locle, August 1885), that light penetrates water much deeper than the bottom of nearly all our fresh water lakes. Whilst it cannot go beyond 400 metres in the sea, we still find certain marine animals provided with eyes at several thousand metres depth. This singular fact is explained by the phosphorescence of a large number of marine animals, phosphoresence which must light up these great depths.

[2] Plateau, *L'instinct, etc., mis en défaut par les fleurs artificielles.* Association française pour l'advancement des Sciences. Congrès de Clermont-Ferrand, 1876.

A nest of humble-bees which I have put for several years in a window of the façade of a house has been the cause of my noticing the difficulty the bees had in distinguishing this window from other windows in the façade when returning from their excursions. Especially in the early visits they flew for a long time over the other windows before discovering the right one. Lubbock (*l.c.*) describes various analogous observations.

September 1st, 1877, was a fairly fine day after long rain. Many humble-bees (*Bombus terrestris*, *pratorum*, etc.), females and males, visited two clumps of red, white, and blue bindweed, mixed with several other flowers and situated on each side of the entrance to the lunatic asylum of Munich. These humble-bees appeared very hungry and visited all the bindweed. I took six there ; I cut off the two antennæ at the base and let them fly. At the end of six minutes one of them (a male) returned and visited eight to ten bindweed flowers one after the other. Each time it flew directly towards the flower, without hesitating a second. I retook it, made sure of the complete absence of the antennæ and released it. This time it made a circuit in the air and returned forthwith to the bindweed which it recommenced to visit as before.

I then took other humble-bees and with scissors cut away all the front part of the head as far as the compound eyes. Then I pulled out the rest of the lower lip drawn in behind and removed it together with the entire pharynx. I had thus removed all the nerve terminations of the mouth, tongue, and pharynx, including the palpi. But, according to Wolff, the sensory organ of the pharynx should be the organ of olfaction, which, as we shall see, is false. The so-called olfactory organ of Wolff was, naturally, completely extirpated and could be prepared from the part removed. Further, the extirpation of the pharynx must prevent completely all respiration of the head, such as Wolff described (*l.c.*). Despite this, the humble-bees thus mutilated flew quickly, seeing and moving their antennæ, which could not be the case if their heads had been asphyxiated. I released them and they flew off. Two of them, two males, returned at the end of a certain time and recommenced, like their intact comrades, to fly from flower to flower. But they only stopped a few instants at each flower, because, despite their hunger, these unhappy bees, deprived of mouths, were unable to eat. Nevertheless, they could not understand the cause and only abandoned each flower to fly to another and recommence their fruitless attempts.

At the same time several humble-bees, deprived of antennæ, returned to the bindweed, flying from one to the other with, if possible, more precision than intact bees.

The afternoon of the same day I repeated my operations, in the two ways indicated, upon numerous humble-bees. None returned.

On September 2nd it rained, but on September 3rd the weather was fine. I returned to the bindweed, where I found several bees, males and females, from whom I had removed the two antennæ two days before. They flew from flower to flower with astonishing rapidity and precision

I then caught several male *Bombus pratorum*, which visited the bindweed very rarely and nearly always plundered the rare flowers of an exotic blue veronica. I removed from them *both antennæ: the forepart of the head and the pharynx* in the way described above. One of the two, once released, merely made a turn in the air, returned immediately to the flowers and flew straight towards the veronica. It vainly tried to eat, going from flower to flower and from clump to clump. It then tried, no less vainly, several bindweed flowers and ended by taking itself off. It behaved exactly as did those operated upon on

September 1st. Soon a second *Bombus pratorum* arrived, doubly mutilated, and it did exactly as the former, and flew straight for the veronica, but did not go to the bindweed. I took it and made sure of the absence of the two antennæ and forepart of the head. The small females of the humble-bees operated upon at the same time never returned. It seems that they were more conscious of their mutilation than the males, because the workers and females are always much more intelligent than the males among the social hymenoptera. I have also shown that the brain properly speaking (*pedunculate bodies*) of worker ants is much larger than that of males, although the latter have larger bodies and larger cerebral nerves (optic and olfactory) than in the species examined (*l.c.*).

I similarly mutilated several *Pollistes gallicus* (a kind of wasp) which visited some mignonette. They behaved exactly like the humble-bees. Some returned, flew at once to the mignonette, where they vainly tried to feed.

During these experiments (of which I regret the inevitable cruelty), and more still when I cut the antennæ of wasps and bees, I usually noticed that the loss of the antennæ, far from rendering these insects uncertain in their flight, seemed to augment their precision. They no longer poised themselves to right and left in the air before alighting, as did most often the wasps especially, but they flew in a straight line towards a point and alighted immediately, like flies and dragon-flies. The difference of behaviour before and after removal of antennæ is specially striking in wasps of the genus *Vespa*. All of which seems to me to show that the hovering during flight allows these insects to smell certain substances with their antennæ. This may be why this hovering is much more marked in wasps that have better sense of smell and see worse than in bees which see better and smell worse. However, new experiments are necessary on this subject.

The above experiments and observations clearly show that it is only the compound eyes which thus direct the flies, the lepidoptera, the cockchafers, dragon-flies, humble-bees and wasps in their flight and the hydrometra in their nimble gambols on the surface of the water. It is with this organ alone that these insects distinguish, whilst on the wing, colours, objects (especially in motion), distances, and by means of which they find their way in the air. Odours, as we shall see, are capable of attracting certain winged insects in a certain direction (for example, the *Calliphora vomitoria* already cited), but without eyes they cannot find their way in the air, whereas we shall see that after losing their other principal senses, among others that of smell, they are yet perfectly capable; only they cannot then smell hidden substances. Finally the above facts enable us to understand to some extent the clearness of vision in some insects as well as their faculty of distinguishing colours (Lubbock), to see far and near, and to measure distances.

CHAPTER III

VISION (*continued*)

Colour Vision; Ultra-Violet Vision; Vision of Form

NO modification of first-rate importance needs to be made in what I wrote in 1878, which is recapitulated in chapter ii. The chief discovery which we have to note since then has been made by Lubbock.[1] This author found that ants perceive the ultra-violet rays of the spectrum, which we are unable, or almost unable, to perceive. He took, in a very ingenious manner, advantage of and utilised the fear that ants have of leaving their pupæ in the light. Some ants, in an artificial nest, had put their pupæ, thanks to Lubbock's precautions, in a division situated under a piece of glass which could be uncovered at pleasure. When the glass was uncovered, the ants carried the pupæ away; when it was covered up they brought them back, especially when a little heat was concentrated thereon. Lubbock then placed his ants in a darkened chamber and passed successively over the uncovered glass the different colours of the solar spectrum. The ants allowed the pupæ to remain under the red rays, but carried them off when any other rays rested on them, seeming specially disturbed by the violet and even more by the ultra-violet rays, which are invisible (or nearly so) to man. When the ultra-violet part of the spectrum was directed from the darkness on to the glass the ants quickly carried off the cocoons. Solutions which, transparent to our eyes, absorbed the ultra-violet rays, had on the ants the effect of shade. This fact is of very great general interest, for if it does not precisely demonstrate a sixth sense, it at least proves that ants perceive a variety of light which we cannot perceive as such, whilst they do not appear to perceive red as we perceive it.[1]

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[1] Lubbock, *Ants, Bees, and Wasps*. London, 1882, p. 207, *et seq*.

To what extent do insects perceive form, that is to say, the dimensions and contours of whatever catches their eye. It is very evident that they do not perceive it as clearly as we do, but it seems to me undoubted that, when they possess well-developed compound eyes, they appreciate size and *more or less distinctly the contours of objects.* How could they otherwise measure distances, alight from the wing on to objects with so much precision, orient themselves so well (find again with certainty such and such a stone, some particular corner of ground, some special bit of wood) despite the absence of the sense of smell (compare the first part of these experiments with those which concern the sense of smell)? The following experiment, conducted after Lubbock's method, seems to me to show that wasps and humble-bees distinguished the shape of objects, as is, further, the opinion of Lubbock also.

I placed a wasp (*V. germanica*) on some honey put on a disc of white paper a little more than 3 centimetres in diameter, the whole being put on my trunk. After gorging with honey, the wasp flew off and soon returned straight to the white paper, where she gorged herself a second time with the honey. I then replaced the disc of white paper by a similar disc, but without honey, and placed the first disc (with the honey) at the side, about 2 inches away. The wasp returning, went first to the empty disc (in the old place), then, finding nothing on it, raised herself a little in the air, hovered two or three times, saw the other disc, went for it, and gorged herself anew with honey.

I profited by her fresh absence to put the honey this time on a cross of white paper 11½ centimetres long in all directions and with branches 2½ centimetres broad.

The cross and the disc without honey were placed close to one another on each side of the place to which the wasp came for her repast. When the wasp returned she searched a little and found the honey quickly. I thought the cross differed too little from the disc, and I cut out some bands of paper 10 centimetres long and 8 millimetres broad.

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[1] Graber (*Sitzungsber. der math.-naturn. Classe der K. Akad. d. Wissensch. Wien*, Bd. lxxxvii. Abth. 1, 1883) doubts the results of Lubbock, and believes that the perception of the ultra-violet takes place by the skin. He shows by ingenious experiments that worms and blinded tritons will perceive light by the skin and even differences between colours.

After the departure of the wasp, I removed the cross and placed on each side of the place where it had been, at about the same distance from the latter (one or two inches), on one side a white disc without honey, and on the other side one of the bands with honey. As soon as the wasp returned, she flew straight to the white disc, where she vainly searched for the honey a long time. Then she searched the middle, on the grey bottom of the trunk where the cross had been, and, finding nothing, flew away. But she returned quickly, searched anew on the disc, then on the old grey place, then she began to smell and hunt about to right and left so well that she ended by finding the honey.

I then put another narrow band without honey at the side of the first (which I removed), and placed some honey on the big cross on the other side at the same distance from the place where the wasp came to eat. The animal returned and flew straight to the new narrow band. Finding nothing there, she searched and quickly found the cross.

It is interesting to see the same wasp (she brought no companions) remember the paper on each occasion at which she had eaten on the last of her visits, and judge of it *by its shape and size*, for I replaced the honey paper every time by another paper cut on the same model.

The following day my wasp returned twice following to eat at the cross left at the same place. I then took her and removed both antennæ. She flew away, but returned half an hour later to eat, always at the cross, which I had left in the same place. After her departure I put a similar cross at the side of the first cross, but without honey; then on the other side a narrow band with honey; finally removing the honey cross. The wasp returned, flew straight on to the cross, alighting just in the centre (where the honey was on the other cross), and searched it vainly for a considerable time. Then, although deprived of antennæ, she began to search, doubtless recollecting that the white papers on which the honey was had already often changed in place and aspect.[1]

She quickly found it on the narrow band, not without, however, having passed within a few millimetres of it two or three times without noticing it, which would not have happened to her if she had her antennæ. She only noticed it when her mouth touched it.

Having that morning found a humble-bee (*Bombus*) slightly benumbed by the temperature, still cold, I put him on a disc painted blue and furnished with honey, placed on my trunk in my room. After being refreshed, he wanted to fly away, but his wings failed him ; he fell to the ground and climbed on to my trouser (black), where I allowed him to walk for a time. Then I put his blue disc before him and he climbed on to it and ate anew. I replaced him gently on the trunk and soon after he flew away, not without making several turns in the air to examine the locality before leaving it, as humble-bees always do in like case. After a certain time my humble-bee returned, flying towards the window, but could not find the trunk. I then went out by a French window close to the window (in the same façade). The humble-bee met me just there and flew to my trouser, which he appeared to recognise, for he alighted upon it and started to investigate.

I then re-entered the room without his at first flying off. He then commenced to fly in the room, saw on my writing-table a blue disc without honey and threw himself on to it. I then guided him to the trunk, where he found his honey. After eating he flew away, examining the locality anew, then left to disgorge his honey at the nest. From that time he no longer lost himself, and came again several times right to the blue disc on the trunk. I then replaced the blue disc by a narrow blue band with honey, as in the above experiment, and put the blue disc without honey at 9 centimetres distance. On his return the humble-bee flew straight to the disc, although it was at another place. But he only made a turn there and went to the narrow band, where he feasted on the honey. I then gave him the disc of honey again, to which he made several journeys. Two hours later I again put the narrow band with honey where the honey disc had been, and I placed a blue disc without honey at 6 centimetres distance. This time the humble-bee went first to the narrow band (at the old spot); but he scarcely stopped there, took no notice of the honey, and flew to the empty blue disc, which he examined in all directions and made a tour of two or three times. Then he flew to the narrow band, where he found the honey. It can be seen by this that colour was the important thing to him, and that when one blue object had no honey upon it the other attracted him at once.

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[1] The inconvenience of these experiments is that one cannot repeat them too often on the same insect without their losing their clearness and value. It is clear that when the form of the paper is changed several times following the insect remembers having found honey sometimes on one shape, sometimes on the other. It will finish by scarcely allowing itself to be deceived. It is therefore necessary to be prudent, to take time, not to scare the insect away, to observe very carefully, and to note observations immediately.

I repeated a well-known experiment of Lubbock on this humble-bee; I replaced the blue disc several times by a red disc with honey, and placed the blue disc without honey at 4 or 5 inches distance. Each time the humble-bee went straight to the blue disc, explored it all over, and could not find the honey on the red ground, although it was at the accustomed spot.

One single occasion he found it by accident in hunting about; but he scarcely tasted it, he was so dominated by the idea "*honey* and *blue*," and he began to search afresh on the blue, without ever again discovering the honey on the red. It is evident to me that, generally speaking, humble-bees have a much worse memory for places than wasps. It is necessary for them to have been to a locality several times (or to have seen an object several times) for them to know how to find it again without much hesitation, whereas a single inspection is enough for wasps.

The influence of colour is certainly most striking. The humble-bee could not find the honey on the red disc even when I guided him to touch it, putting it under his nose; he continued to search on the blue with a perseverance that had little intelligence about it. It is very evident that he perceived the colour infinitely more intensely than the form of the paper.

I have also verified another of Lubbock's results very clearly: although humble-bees (like honey-bees) especially distinguish colours, wasps pay them very scant attention, and, on the contrary, rely specially upon the locality, which they always recognise admirably. When I replaced the blue paper of honey by a red paper of honey, putting a blue paper without honey at the side, a *Vespa rufa* which had come two or three times to the blue paper went straight to the red paper because it was in the old place. Scarcely once or twice did she examine the blue paper without honey for an instant. One cannot deceive wasps with colours as one can hive-bees and humble-bees, which, however, does not suffice to prove that they distinguish them badly. But when the coloured paper with honey is removed to some considerable distance (3 decimetres, for example) from the place where it was previously to be found, the wasp vainly seeks it at the old place; she does not find it, or only reaches it by chance while searching its neighbourhood,[1] and with the help of the sense of smell. The humble-bee, on the contrary, guided by the colour, finds it quickly. The fact that wasps guide themselves so well when flying when deprived of their antennæ and, as Lubbock has shown, without distinguishing colours very clearly, is one of the best proofs of the fact that they see the form and contours of objects. The objection that another sense may serve to guide them is valueless, for we have seen that when their faceted eyes are varnished they can no longer guide themselves, whilst they can direct their flight without antennæ, mouth, or pharynx as well as with these organs.

Since 1878 Exner has published two new works on compound eyes.[2] He has given the history of the subject, and shows that in the glow-worm the crystallines are so closely adherent to the corneæ that they can be removed with the latter and both directly examined with the microscope. One can then be assured that it forms no image, but simply a luminous point at the bottom of each crystalline. The tiny images seen by Leeuwenhoek and Gottsche[3] are only formed by the corneæ when the crystallines have been removed; the crystalline destroys them. These images have therefore no more value than that produced by a little drop or by any other transparent convex body.

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[1] Each time that one of these insects has searched vainly for a desired object for a certain time at the place where it thinks it first saw or recognised it, it starts exploring the neighbourhood, but always more rapidly, in a less exact and less careful manner.

[2] Exner. (1) *Die Frage von der Functionsweise der Facettenaugen.* Biologisches Centralblatt, Bd. i. S. 272 (1881-82). (2) *Ein Microrefractometer.* Archiv f. microscop. Anatomie, Bd. xxv.

[3] Gottsche, Müllers Archiv, 1852.

Exner also shows that the long and curved crystallines of the genus *Phronima*, quoted by Oscar Schmidt[1] as objections to the theory of J. Müller, can, despite their curvature, convey light to the retinules very well, and confirm the theory of J. Müller instead of upsetting it. Finally he refutes various theories of Notthaft,[2] among others that which seeks to establish the hypothesis that insects judge distances by the decrease in the intensity of light as the object is more remote. Exner believes that the movement of the insect itself when flying aids it in measuring distances. He also sees, in the fact that the common visual field of the two eyes is greater in insects than in vertebrates, a degree of superiority for the appreciation of distance. It appears to me that from the latter point of view one can scarcely compare our binocular stereoscopic vision (convergence of axes and distinct images) with the mosaic sight of the faceted eye. Further, it is not exactly true that the common visual field of the two eyes should be greater in all insects than in vertebrates. It varies enormously according to the species (enormous in dragon-flies, *nil* among certain *Cryptocerus*, Fig. 6 *a* and *b*), as, besides, it also varies among vertebrates. In the second work Exner corrects, by means of his microrefractometer, an error which he made in his original calculation of the refraction and focus of the cornea of *Hydrophilus*; this fact, however, does not alter his opinion on the vision of faceted eyes.

We here note that the opinion of Gottsche, according to which insects see as many distinct images as they have facets, had the approval of Max Schulze,[3] Leydig,[4] Dor,[5] and most naturalists, perhaps Joh. Müller himself (annotation to the works of Gottsche).

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[1] Oscar Schmidt, Zeitschrift f. Wissensch. Zoologie, Bd. xxx. Suppl.

[2] Notthaft, Abhandl. d. Senkenberg'schen naturf. Gesellsch., Bd. xii.

[3] M. Schulze, *Untersuch. üb. d. zusammengen. Augen der Krebs u. Insecten.*

[4] Leydig, *Das Auge der Gliedethiere*, 1864.

[5] Dor, *De la vision chez les Arthropodes.* Arch. des Sciences physiques et nat., 1861.

Boll[1] was the first to leave this groove and to return to the theory of Müller. But the works of Grenacher and of Exner, as well as direct biological observation, were greatly needed to give a solid basis to the theory of mosaic vision.

I would offer a few further remarks.

Observation shows that various insects appreciate, even when they are still, the distance of motionless objects. This is seen in the precision with which a male fly will spring from rest on to a female, or the "flying leaps" which many insects make (*Cicindela*, *Buprestis*, etc.). It is true that the movement is instantaneous, but, unless the insect measured its stroke at the moment of moving, it would miss its aim. This demonstrates that movement alone is not sufficient to explain the appreciation of distances.

The fact that insects, especially those that have only a relatively restricted number of facets, see movement infinitely better than objects, is incontestible. In my innumerable observations upon worker ants, I have always remarked that movements, even of objects relatively small (smaller than themselves), attracted their attention. We have, on the contrary, seen that they will pass unnoticing a hundred times to the side of objects, often larger than themselves, and which they are busy looking for. I think that it is even very difficult to show that apterous insects see the contours of objects at all, so nebulous and indistinct is their sight.

When two colonies of ants of almost equal size fight, it is astonishing to see how surely and rapidly enemies recognise one another and lay hold of each other by different parts of the body. But, if one watches closely, as I have quite lately had the opportunity of doing whilst watching a battle between two swarms of *Formica pratensis*, one is convinced that the enemy is only seen at close quarters and when he moves; whilst he keeps still he is only noticed by touching with the antennæ. At a distance of several centimetres even his movements are unnoticed. On the other hand, the same *Formica pratensis* regularly noticed the motion of my arm at a metre above them, because it was much larger: but they did not notice a small object which was moved where my arm had been. A very small ant, *Solenopsis fugax* Latr. (length 2 millimetres, breadth ⅓ mm.), which often lives in the interstices of the nest of a large hostile species, is hardly perceived by the larger species, even when it moves. It must be mentioned that its legs are short and its movements slow. Nothing is more curious than a fight between this species and the large ants.[1]

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[1] Archiv. von Reichert und Dubois-Reymond, 1871.

The dwarfs (*Solenopsis*) courageously attack the limbs of their big foes, which struggle, biting with rage about them, constantly aiming wrong, and only managing quite by accident now and then to catch one of their enemies. The same large ants are, on the other hand, able to distinguish ants a little larger than *Solenopsis fugax*, for example, *Tetramorium cæspitum* (length 2.5 to 3.5 mm.), when they move.

The utility of the frontal ocelli is still an enigma to me in insects which are provided with compound eyes. In certain forms, as in the male *Dorylides*, these ocelli are extraordinarily large. Their cornea has, for example, a diameter of nearly half a millimetre in *Dorylus helvolus* ♂ (Fig. 4 shows the relation of the size of the ocelli, *o*, and the facets of the compound eyes, *f*, in a dorylide, *Eciton cæcum* Latr. [*Labidus Latreilles* Jur.] male, magnified 24 times). Do these large ocelli serve simply to distinguish light from darkness? Do they perceive an image? Here the number of nerve elements is much greater than in a facet or in rudimentary ocelli, and it has no crystalline to make a tube and destroy the image. As we have seen above, the loss of the ocelli does not produce in the insect any derangement which has hitherto been appreciable; this does not speak in favour of the perception of an image. Arthopods which only have ocelli (spiders, etc.) appear to see very badly. Web-spinning spiders recognise their prey by the vibration of this web, by means of touch. A little attentive observation will convince one of this. As to jumping spiders, it appears to me that they only see their prey when they move at a short distance from them. Then they turn in their direction and spring upon them. As they have several groups of ocelli, one might readily suppose that they should be sufficient to indicate to them the direction of the movement perceived, and thus allow them to reach the object by a leap which skims the ground. Moreover, they miss fifty flies for every one they touch, and spin a thread as they walk which prevents them from falling when they jump on a vertical wall and alight badly.

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[1] Forel, *Observations sur les mœurs du Sol. fugax.* Mittheilungen d. schweiz. entom. Gesellschaft, 1869. In this work (the first attempt of youth) I have wrongly attributed to the ocelli (simple eyes) a distinct vision for objects. Nevertheless the observation upon which my conclusion was based (the very distinct sight of the ants [of Europe] provided with ocelli) was well founded. I had, however, forgotten to take into consideration the fact that ants which have three ocelli on the forehead have also the best developed compound eyes.

Dr Eugène Bleuler, director of the Asylum at Rheinau, to whom I have shown the present work, has made a certain number of observations which he allows me to add and for which I thank him.

1. The *relative position of one object to another* varies for a flying insect more as the objects are brought nearer. This should greatly aid in the estimation of distance, thanks to the special faculty of perceiving the displacement of objects (relative motion).

2. The motion of an object not only must be specially perceived as such, but its shape and outline must be seen with greater distinctness. For example, supposing any protuberance whatsoever of an object only reaches to the border of the visual field of a facet. The motion of the object should either make it disappear or enter the visual field more and more. A variation in the intensity and quality of the brightness would thus be brought about, eventually also in the colour perceived by the facet in question, a variation which will be used by the brain of the insect for the perception of contour.

3. The *attention* of insects should be principally attracted by the motion of objects, because they have not, as in vertebrates, a visual axis for distinct vision, an axis which moves in vertebrates, thanks to the mobility of their eyes, and draws their attention to each across which it travels.

4. The opinion of Notthaft, according to which the quantity of light which a facet receives from an object diminishes as the distance increases, ought not to be absolutely rejected as Exner rejected it. The visual field of each facet necessarily increases with the distance; an object the rays from which occupy, for example, at one decimetre the entire visual field of a facet, will share it at ten metres with many other objects,

and this lessens *relatively* the luminous action of this object on the facet.

5. Lubbock's experiments on colour perception do not mathematically prove that it is colours which are perceived. It might be objected that they are, perhaps, only the differences between light and darkness which insects perceive. The colour-blind, even the most complete, can more or less distinguish colours and shades from one another, not as different colours, but by the slight differences of intensity (light and dark).

I am completely in accord with the observations of M. Bleuler, the last of which, however, has only a theoretical value. Certainly Lubbock's experiments are so numerous and the effects of colours on bees and humble-bees are such that the peculiarity of the colour-blind cannot sufficiently explain the facts. My humble-bee, for example, when I had taken the honey from my trunk, sought and very quickly found all the pieces of blue paper in various corners of my room, in whatever surroundings they happened to be and of whatever shape. A colour-blind person could not have done as much. I have seen a colour-blind person unable to distinguish a scarlet rose on green foliage, because the rose was to him as dark as the leaves. But the colour-blind possess the advantage of seeing forms *distinctly*, which is not the case with insects. It is clear that if my humble-bee had been colour-blind he could not have always found blue among many different objects, some darker, others lighter.

At the moment that I was finishing this work I received notice of new experiments of Plateau[1] on this subject, and, shortly after, the author had the kindness to send me his original communication, made this year (1885) to the Royal Academy of Belgium.

Instead of preventing the publication of my work, Plateau's communication impels me strongly in the other direction, for I am obliged to combat his contentions in large part.

Plateau commences by assuming that the theory of J.

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[1] Plateau, *Recherches expérimentales sur la vision chez les insectes. Les insectes distinguent-ils la forme des objets?* Bulletin de l'Académie royale de Belgique, 3me serie, t. x. n. 8, 1885.

Müller as to mosaic vision is definitely rejected, and that thanks to the work of Exner of which I have spoken! This is a complete error. We have, on the contrary, seen that Exner, no less than Grenacher, has rehabilitated J. Müller's theory. Plateau therefore appears to have completely misunderstood the works of Exner, for he even adds that this author has theoretically deduced that insects do not see the form of objects, which also is quite wrong.

Plateau says: " The old hypothesis of J. Müller, *which consists of admitting the production of an image formed in mosaic by the juxtaposition of a series of small partial images of which each occupies the bottom of one of the distinct elements of the compound eye*, is definitely rejected . . . etc." But this is Gottsche's theory and absolutely not that of the mosaic sight of J. Müller. The theory of mosaic sight does not admit of tiny images in each facet, but of a single image in mosaic formed by the juxtaposition of light rays of different qualities perceived by each facet.

Since the theory of mosaic sight appears to be so badly understood, I have endeavoured to give a pictorial representation, approximately demonstrating its principle, in Figs. 1, 2, and 3. We have therein represented a segment of a compound eye of a hive-bee with the facets *a*, *b*, *c*, *d*, *e* (Fig. 1). Suppose that this eye looks towards the blue sky, and that a very small hymenopterous insect, black with a yellow abdomen, passes in front of it, lighted by the sun (in reality the hymenopter is drawn much too small relatively to the facets, but this simplifies matters). Let the sides of the facets be prolonged and suppose that these prolonged sides represent the respective limits of their visual fields (in reality the visual field of each facet is more considerable and receives yet more oblique rays that the cornea refracts and brings to the retinule; our supposition, therefore, is only relatively true). Suppose the hymenopter in the position figured (Fig. 1). Its head and thorax occupy the visual field of the facet *d*, its abdomen that of the facet *c*. The visual field of the facet *b* will be occupied partly by the blue rays from the sky, partly by the yellow rays of the extremity of the abdomen of the hymenopter; this (since no image whatsoever can be formed on the retinule) forms for the insect a mixture of yellow and blue, probably a green shade. The other facets only receive blue rays.

Let us carry that on to the mosaic of the visual fields of the facets, and we shall have the image *b′*, *c′*, *d′* of Fig. 2, a rough sketch, it is true, but yet a very vague shape recalling that of the insect and the order of its colours. The facet *b′* will perceive probably a green more or less blue or yellow according as it will receive more of the rays from the sky or from the insect.

In reality the insect will not see the hexagonal image of Fig. 2, nor the blue of the sky divided into hexagons, for—

1. Habit and heredity will have taught it to take no note of the limits of the facets, if ever it was capable of perceiving them.

2. The visual fields of the facets are more or less confused at their boundaries owing to oblique rays (which come to the retinule in numbers the greater as the facets are larger and less deep and as the distance increases). This produces a fog of colours or mixed lights around the central visual line of each facet, and an image something like the one in Fig. 3 would probably be what our bee would see, or at least what would serve as a basis to its perception. Hazy as it is, this image will yet be a representation of form.

Now suppose that an insect is a dragon-fly having 20,000 facets, and that he sees passing in front of him a fly which gives out rays to the visual field of 1000 of these facets (according to the distance at which it will pass, it will give out to a greater or less number). Here we have long, very narrow facets, distinctly isolating a small luminous pencil. The number of rays diffused over the confines of each facet will be very limited, especially if the fly is near. It is useless to make another sketch to show that in this case the number of little hexagons occupied by the rays proceeding from the different parts of the fly will be such that a true and sufficiently distinct image, still a little hazy, should be perceived by the dragon-fly. This image should represent, with slightly vague contours, the different parts of the fly. This is precisely what Exner and Grenacher found.

If anyone objects that Exner has not absolutely demonstrated the destruction of the image by the crystalline, and that it could still be thought to form a small *part of an image* at the fundus of each facet, the whole of these portions of images in juxtaposition forming an entire image in mosaic, we reply that two facts render this explanation untenable:—

1. The fact that the augmentation of the number of facets enormously increases the distinctness of the sight of insects, which would not be the case if each retinule were capable of perceiving a distinct part of the image.

2. The fact that the genus *Phronima* has curved crystallines (Oscar Schmidt), which makes the thing quite impossible in that instance. We refer, further, to the arguments of Exner and Grenacher cited above.

But passing on to the experiments of Plateau, who thought to show by their aid that insects do not perceive form. These experiments are simple. Plateau contrived, in the closed shutters of a black chamber, a single opening of sufficient size to allow several insects to pass it flying. At a certain distance he made a group of orifices, clefts, and holes, allowing together as much light to pass as the first hole by itself, but too narrow to let insects pass. Plateau then released various diurnal winged insects in the chamber, and found that they flew without distinction either to the single orifice which allowed them to get out or to the group of little holes which kept them prisoners. The whole of the small orifices naturally made a much larger surface than the single hole. If one of the holes allowed more light to pass altogether than another, it is to the first that the insects fly especially, caring little whether this be a latticework or a single hole. Plateau constantly measured the amount of light by Rumford's photometer to guard against any objection of inaccuracy. I do not for one second doubt the accuracy of his results, which I should have been able to predict in advance. I have only one objection, but that a capital one, to make: The experiments of Plateau absolutely do not demonstrate what he wished to demonstrate, but they prove only that Plateau attributes to insects a faculty for reasoning that they do not possess.

I go further, and believe that more than one vertebrate which has eyes like our own would in like case commit the same mistake. Plateau takes no account of the astonishment or fear of an insect placed in such a situation. He forgets the thoughtlessness, or rather the extreme feebleness, of reasoning in an insect, and asks it to know how to judge by a glance, at such a distance, whether it can or cannot pass such a hole. He further asks that the insect shall see, or rather divine, that the holes are all on the same plane and separated one from the other by solid barriers which cannot be displaced. It is to ask of insect eye and insect brain what man himself cannot in certain cases distinguish, for there are plenty of people who deceive themselves at a distance of several metres as to the size of a hole, and cannot gauge whether it can or cannot give exit to their bodies. Finally, Plateau did not show these insects objects, but holes allowing light to pass. But it is sufficient to reflect that diffused light comes obliquely, and that, as we have said as regards mosaic sight, to understand in such case insects can only distinguish more or less hazily the bars separating the holes. One ought, therefore, to recognise the fact that insects would fly rather towards the more luminous source, without studying the shape of the holes, and one single thing astonishes me—that Plateau expected anything else.

We cannot judge of whether insects see or do not see forms, except by deceiving them when they are searching for something, while we carefully exclude other sense organs. They must be able to distinguish the object in question by shape and size only, but they must be obliged to distinguish it in order to attain their end. Above all, an experiment should never be attempted that requires reasoning for its proper accomplishment, and too much importance should not be attributed to negative results, which may depend on other than visual causes.

I may be permitted to point out that, in the first part of this work, published in 1878 in German, and quoted elsewhere (*Palpes des insectes broyeurs*, 1885) by Plateau, I have already shown by means of observations and direct experiments upon living insects that their sight is almost always indistinct, and that this naturally extends to form (for example, the story of the wasp chasing flies and being deceived by a nail, etc.).

Plateau further verifies the fact that the presence of ocelli in no way modifies the results of his experiments, and concludes that ocelli are only rudimentary organs. I prefer to call them, by the term which we have hitherto employed, accessory organs, at any rate the frontal ocelli, which are decidedly not primitive rudiments, but organs of secondary formation.

Plateau further concludes from his experiments that diurnal insects have need of a fairly bright light to guide themselves and cannot do it in semi-darkness, a fact which has often been wrongly attributed to lowering of temperature. To begin with, I believe that it has always been known that the diurnal lepidoptera do not fly by night, whilst many nocturnal lepidoptera on the contrary scarcely fly except by night. Further, it has always been known that on a warm night earth and air swarm with active insects, and that consequently the difference between the ways and habits of nocturnal and diurnal insects should be attributed to light and not to heat, the influence of temperature being the same for one as for the other. But Plateau's conclusion is in itself too absolute. From the fact that various diurnal insects do not fly when the sun ceases to shine or when the light is less intense, it cannot be concluded that they are not capable of guiding themselves. There may be other reasons, of adaptation to the conservation of the species, for example, that keep them from flying when the acuity of their vision is diminished by the diminution of the light. Still, there are certain insects (*Sphinx*, *Melolontha solstitialis*, etc.) which only fly at a certain regular hour of the evening, and only during a very short time. These same insects can guide themselves very well in flight, in case of need, at other hours of the day, in a very different degree of light. The butterfly has probably the idea that it is dangerous for him to fly when the weather is too dull. However, it is very possible that Plateau may be in great measure right: the very small facets of the convex eyes of essentially diurnal insects have very long and narrow crystallines which, being better isolated, allow less light to pass. This fact has already been pointed out by Max Schulze apropos of nocturnal lepidoptera (*vide supra*). I am persuaded that winged insects of twilight and nocturnal habits direct themselves in flight by the aid of their eyes as well as diurnal insects, cats and owls.

Finally Plateau, after having spoken in the course of his preliminary notice only of the non-perception of form, concludes his dissertation in these words: "In conclusion, they (insects) do not distinguish the shape of objects, *or they distinguish it very badly*." With the last proposition we are able to agree with certain reservations.

We may sum up what we know as to sight in insects thus:—

1. Insects guide themselves in flight almost entirely, and on the ground partly, by means of their faceted eyes. The antennæ and the buccal sensory organs cannot help in aerial steering. Their extirpation does not in the least diminish their faculty of guiding themselves when on the wing.

2. The theory of mosaic sight of J. Müller is the only true explanation. The retinules of the compound eyes do not receive any image, but each a single luminous pencil more or less distinct in origin from that of its neighbours. The theory of Gottsche is absolutely false (J. Müller, Grenacher, Exner).

3. The larger the number of facets, and the longer the crystallines, the more distinct is the sight (J. Müller, Exner) and the longer is the relatively distinct sight.

4. Insects perceive the motion of objects particularly well, *i.e.* the displacements of visual images relatively to the compound eye. They therefore see better when on the wing than at rest, for during flight the image of immobile objects is displaced relatively to the eye (Exner). This perception of the mobility of objects diminishes (as does the relative displacement to the eye) according as the distance increases.

5. Insects only distinguish the contours and forms of objects in a more or less indistinct fashion, the more indistinct as the number of facets is less, as the crystallines are shorter, as the object is further off, or as it is smaller. Insects which have large eyes with several thousands of facets see form fairly distinctly.

6. Insects appreciate the direction and distance of objects very clearly during flight, by the aid of their compound eyes. This is at least correct for near distances. They can also appreciate, even when at rest, the distance of immobile objects.

7. Certain insects (bees, humble-bees) distinguish colour clearly and recognise colours better than forms. Among others (wasps) the perception of colour appears, on the contrary, to be

very rudimentary. Ants perceive the ultra-violet rays (Lubbock).

8. The ocelli appear to give a very incomplete sight and to be only mere accessories in insects which possess compound eyes. They yet may serve, perhaps, for the sight of very close objects in an obscure medium; the fact that they are found especially developed in those aerial insects which inhabit complex and dark nests where they have to guide themselves tends to verify this. The ocelli would then be a slight complement to smell (see experiment of 1886).

9. The rapidity with which the increase of distance diminishes in regular proportion the distinctness of contours must necessarily help insects to appreciate distances (1900).

PLATE I

EXPLANATION OF THE FIGURES

Figs. 1, 2, and 3. See explanation in text. *Fig.* 1 represents an extremely small hymenopterous insect flying before the compound eye of a bee. *Fig.* 2 represents the simplified scheme of the theoretical image that it produces in this eye. *Fig.* 3 should give an idea of the manner in which the image would, perhaps, be perceived by the bee in reality.

Fig. 4. Head of *Eciton cœcum* Latr. = *Labidus Latreillei* ♂, seen from in front, to show the relative size of the eyes and the frontal ocelli. The diameter of an ocellus is about 33 times as large as that of a facet. × 24 times about. *f*—Faceted eye; *o*—frontal ocelli. It is the worker that is blind, not the male!

Fig. 5. Head of *Eciton lugubre* Roger (soldier); to show the position of the two lateral ocelli (*ol*), which, in this genus, are the homologues of the faceted eyes. × about 4½ times.

Fig. 6. Head of *Cryptocerus discocephalus* Smit. *a*—Front view; *b*—hind view to show the impossibility of a common visual field for the two eyes in this species. It must not be forgotten that the posterior surface of the head is articulated to a large thorax, which makes a common visual field behind the head impossible. × 11 times. *f*—Faceted eyes. In *Fig.* 6*a*, *f* only indicates the direction of the faceted eyes, which are hidden entirely under the edge of the frontal disc.

PLATE

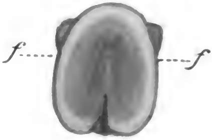

Fig. 6a

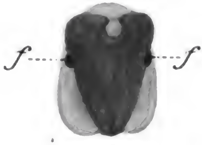

Fig. 6b

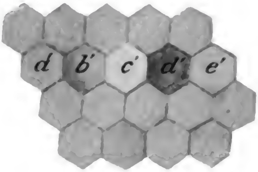

Fig. 2

CHAPTER IV

ULTRA-VIOLET VISION AND PHOTODERMATIC SENSATIONS; RECOGNITION AMONG ANTS

I AM, to commence, able to add, as a complement to my first chapter, that I have varnished the eyes of several moths (of certain *Noctuæ* which hide themselves during the day in dark places and which fly by night, frequently throwing themselves onto lighted lamps). These moths were found as clumsy at flying as the diurnal insects; they knocked themselves against the wall and fell to the ground.

Before leaving the sense of sight, we have to concern ourselves with a question recently raised by Vitus Graber,[1] that of the sensations or perceptions called *dermatoptic*, or, better, *photodermatic*, studied by means of the so-called photokinetic reaction of animals (their change of position due to luminous perception). Graber shows that earthworms, even when decapitated, and tritons from which he had removed the eyes, leave the lighted compartment of a receiver to repair to the dark compartment. These same animals leave the compartment lighted by daylight to enter one where the ultra-violet rays are intercepted by sulphide of carbon. They leave blue to go under green or red. Briefly, they behave as if they see, and always leave the light with the shorter waves to go under that of which the waves are longer; they leave the chemical spectrum to go towards the calorific spectrum. Graber thereby concludes that these animals perceive light by the skin, that the action of the light reaches their "*sensorium*"; we prefer to say "that it is felt by their central nervous system." Th. W. Engelmann[1] demonstrates the same action of light on the lower organisms. Later he finds that the cones of the retina contract in the frog not only under the direct influence of light, but even in the unilluminated eye when the light acts on the other eye, and even in both eyes completely obscured when direct solar light is made to act for a quarter of an hour on the skin of the legs and belly, kept constantly wet. This last fact shows irrefutably a transmission of luminous cutaneous stimuli to the retina by the intermediation of the nervous system. Finally, Graber recalls the fact that the actinozoa, certain blind mollusca (*Dentalium*, according to Lacaze-Duthiers), the protozoa (according to Haeckel, *Kosmos*, Bd. iv.), etc., give undoubted proofs of reactions, either agreeable or disagreeable, under the influence of light, which some seek and others avoid. Among marine animals, Graber finds some species photophobic and others photophilic. The latter then prefer blue to red, etc., seeking the parts of the spectrum in reverse order.

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[1] V. Graber, Biologisches Centralblatt, Bd. ii. No. 4, p. 114. The same: *Fundamentalversuche über die Helligkeits- und Farbenempfindlichkeit augenloser und gebendeter Thiere.* In Sitzber. der math. naturw. Cl. der K. Akad. der Wissensch. Vienna, April 5, 1883. The same: *Grundlinien zur Erforschung des Helligkeits- und Farbensinnes des Thiere*, 1884. The same: Biologisches Centralblatt, Bd. v., Sept. 1, 1885.

One cannot, therefore, doubt the existence of photodermatic perceptions in certain animals, although Engelmann does not appear to have taken great care to eliminate the factor of heat, which is always closely allied to that of light. Graber has, nevertheless, taken care to expose the cases containing his earthworms to diffuse light and to the north. He has even made a comparative experiment with a paraffin lamp and a solution of alum; when the difference of temperature did not exceed one degree centigrade, the blinded tritons did not react.

Almost all the animals upon which experiments have been carried out are either aquatic or at least live in damp places. Their skin is damp. Now one knows the part played by chromatophores in many of these tegumentary structures. Nevertheless, Graber has obtained results which are identical in blinded specimens of *Blatta germanica*, nocturnal insects somewhat soft, it is true, but the skin of which is chitinous.

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[1] Th. W. Engelmann. *Ueber Licht- und Farbenperception niederster Organismen.* Pflügers Archiv f. Physiologie, Bd. xxix. p. 387, 1882. The same: *Ueber Bewegungen der Zapfen- und Pigmentzellen der Netzhaut unter dem Einfluss des Lichtes und des Nervensystems.* Pflügers Archiv. Bd. xxxv. p. 498, 1885.

Graber thinks that the perception of the ultra-violet rays, which Lubbock first demonstrated in ants, is wholly or in part photodermatic. He quite acknowledges that the reaction to light of animals possessed of eyes is stronger and more lively, but he believes that it depends upon the fact that blinded animals have more trouble in finding their way (this explanation is not very logical, since it would prove that they see).

Be that as it may, the possibility follows from all these facts that the reaction of ants to the ultra-violet may be dermatic, when they do not act by means of sight, properly speaking ; so that one no longer has the right to say, with Lubbock, that they see a colour which we do not see. I have made some very delicate experiments with the object of elucidating this problem. Before describing them, I may be allowed to point out that Prof. L. Soret[1] of Geneva has demonstrated by experiment that the refracting media of the vertebrate eye, the lens in particular, absorb the ultra-violet to a high degree, *i.e.* the ultra-violet rays exceeding the solar U ray and almost all those situated between Q and U. Only the rays of H to Q partially reach our retina, but we do not perceive them as a particular colour. Nevertheless, certain young persons see in very dark violet that which is ultra-violet, *i.e.* invisible for others. On the other hand it has been observed that the ultra-violet rays can be perceived as a grey-lavender ground on which the rays L to Q of the solar spectrum appear a little more distinct and even up to the ray S in those who have been operated upon for cataract (Chardonnet). The last fact seems to show well that if we do not see the ultra-violet its absorption by the refracting media accounts for a good deal.

My plan is very simple. I wished to follow Graber's experiments on the photodermatic sensations of cockroaches, etc., to see whether the ultra-violet rays incommoded ants which had been deprived of sight as much as before the operation. But the experiment is very difficult, seeing that it is not possible to extirpate the eyes of ants without killing them or making them too ill for the observations to retain the least value. It will be objected—why choose ants? To that I would reply that I knew their habits, and that it was their complex habits precisely that allowed me to vary experiments in a very advantageous way, as will be seen. Such variation could not have been made with stupid beings like earthworms, etc. The following are my experiments.

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[1] J. L. Soret, *Recherches sur l'absorption des rayons ultra-violets par diverse substances*, 5me Mémoire. Archives des Sciences physiques et naturelles de Genève, x. p. 429, 1884.

I had at first chosen a large species, *Camponotus ligniperdus* Latr., which has, besides its size, the advantages of not possessing frontal ocelli. Then I tried to varnish the eyes completely. As ants hasten to brush away the varnish with the comb of the anterior feet, I chose an old opaque white varnish well dried (Frankfort varnish [Hirsch-Apotheke] for microscopic preparations). Dissolving this varnish in a little chloroform and rapidly putting it on the eye of the ant with a cataract needle, while I held the feet, it dried very quickly, adhering very solidly, so that the ant brushed in vain to get it off. This proceeding succeeded very well. Only I was obliged to make certain every time with a magnifying glass that each eye had been completely covered with a thick layer of varnish. Unfortunately the layer of varnish is never thick enough entirely to intercept a rather strong light, even when diffuse. I have endeavoured in my last experiments done on some *Formica sanguinea*, several workers and one female *Formica fusca* L., to obviate this inconvenience by adding to my varnish a strong dose of tar, quite dry, in such a way as to make it nearly black. I have thus obtained a considerable but not absolute opacity.

It is very interesting to observe the behaviour of ants thus nearly or completely blinded. We have seen, in the first part of these researches, that flying insects completely lost the faculty of guiding themselves in the air when their eyes were varnished, although the loss of the antennæ does not change, or scarcely changes their progress. Here we see diametrically the opposite, as I have already noted in my *Fourmis de la Suisse*, 1874. But then I was only able to show that ants minus their antennæ have lost the faculty of directing themselves or of recognising their friends. This time I have been able to prove in an irrefutable manner that the varnishing of their eyes neither hinders them from guiding themselves, nor from distinguishing their friends from their enemies, nor from taking care of their larvæ and their pupæ. My *Camponotus* with varnished eyes quickly attacked and killed a *Formica fusca* put in the midst of them, seizing it almost as adroitly as those which had the use of their eyes. They removed a heap of larvæ from one corner of their receiver to another with as much precision as with their eyes. I later established them with the unvarnished remainder of the colony in a hole on the outskirts of a wood. I then could see my varnished-eyed workers find alone the entrance to the nest, fight, and, briefly, conduct themselves almost like normal workers. Nevertheless they were altogether less active at work and kept more in the open air (in the light, outside the nest) than the others. While the unvarnished saw the approach of a forceps or whatsoever object was held at a certain distance, and retired menacing with their mandibles, this was not the case with the varnished ones, who only perceived it when quite close (by smell or touch). It is also important to note that when the ants are under the glass and when they are lit up suddenly (after darkness), those which have varnished eyes remain still, whilst the others, frightened, move away quickly.

In order entirely to intercept the ultra-violet rays, I use a case one centimetre thick, filled with a concentrated aqueous solution of Esculine,[1] on the recommendation of Prof. L. Soret of Geneva, the well-known authority in such matters, who has very kindly assisted me with his advice. The sulphide of carbon used by Lubbock, M. Soret assures me, has the inconvenience of allowing the infra-red calorific rays to pass, and it only completely absorbs the ultra-violet when it is impure and yellowish. To allow as much ultra-violet to pass, whilst absorbing as much as possible of the other rays of the spectrum, I have, following the advice of M. Soret, used, as Lubbock did, a glass of dark cobalt violet. To eliminate the heat rays as much as possible, I use a layer of water 6 to 8 centimetres thick, which, according to M. Soret, sensibly stops the half of the total heat of solar radiation. A rather dark red glass serves me for control experiments. It allows especially the calorific rays to pass, but produces apart therefrom an effect on ants analogous to esculine or sulphide of carbon, as Lubbock has already shown. Finally, to obtain complete darkness, I use a sheet of pasteboard 3 millimetres thick.

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[1] The active principle of the Horse-chestnut.—TRANS.

For the sake of abbreviation, we will call the ants whose eyes I varnished "Varnished," and "Normal" the ants which had not been varnished. My experimental method is in no way original; it is simply that of Lubbock, also employed by Graber, with the modifications just pointed out.

First Series

CAMPONOTUS LIGNIPERDUS, NORMAL WORKERS AND FEMALES

I placed my ants, without pupæ or larvæ, in a box 4 centimetres high, 13.5 cm. wide, and 22 cm. long, with a little damp earth in the bottom. The box was covered with a sheet of glass on which I placed, sometimes on one side, sometimes on the other, the cobalt glass, the water, the pasteboard, the case filled with a solution of esculine 1 cm. thick, etc.

1. I put on one side the esculine, on the other the cobalt, and I placed the box in the sun. The ants huddled themselves together under the esculine on the side where the wall of the box made some little shade. I turned the box in various directions, transposing the cobalt and the esculine several times. The ants always went to the side of the box under the esculine.

2. I put on one side the esculine, on the other the pasteboard. The ants always placed themselves in the middle of the box, under the pasteboard. In these two experiments no account was taken of heat, which lessens their value.

3. I put on one side the esculine, on the other the cobalt. I protected the cobalt side from the solar heat by a prismatic bottle full of water. The ants then divided themselves between the cobalt and the esculine.

4. I protected all the wall exposed to the sun by 4 cm. of water. Then I put on one side the cobalt, on the other the esculine. The ants nearly all huddled together under the esculine.

5. The same experiment (4) was repeated under diffused light (reflected or indirect) after transposing the cobalt and esculine. The ants almost all passed, little by little, from the cobalt to the esculine.

6. Experiment 5 transposed, the cobalt being replaced by 3.5 cm. of water. Diffused light (indirect). The ants nearly all passed from the water to the esculine.

In all the experiments I always rearranged matters by placing the esculine on the side where the ants were not, so that their removal gave a clear result.

It may be added that *Camponotus ligniperdus* is a wood ant which loves shade and which fears any extra heat. It may further be stated that these experiments were done in the summer, during great heat.

SECOND SERIES

I VARNISHED THE EYES OF 14 WORKERS AND ONE ♀ OF *CAMPONOTUS LIGNIPERDUS* AND PUT THEM IN THE BOX, ADDING 10 NORMAL WORKERS.

7. Direct solar light, but made diffuse by white clouds. I used on one side two prismatic bottles (with parallel walls), one 6 cm., the other 8 cm. thick.

Result

Water 6-8 *cm. left.*	*Pasteboard right.*
11 varnished workers, 1 varnished ♀.	3 varnished workers.
1 worker clinging to the shady wall.	9 normal workers.

8. The preceding experiment after transposing the water and pasteboard.

Result

Pasteboard left.	*Water* 6-8 *cm. right.*
11 workers and 1 ♀ varnished.	3 varnished workers.
7 normal workers.	3 normal workers walking about.

The normal ants were therefore influenced by the light, which was not the case with the varnished ants.

In the following experiments I inclined the box sufficiently to avoid the production of shade by any of its walls.

9. Repetition of experiment 8 after a quarter of an hour,

without transposition, but following the agitation caused by the shifting of the box.

Result

Pasteboard left.	*Water* 6-8 *cm. right.*
6 workers and 1 ♀ varnished (*sic*).	5 varnished workers.
9 normal workers.	1 normal worker running about.

10. At 2.50, always by direct light, but made diffuse by white clouds, I changed the water and pasteboard of the preceding experiment.

Result at 3 *o'clock*

Water 6-8 *cm. left.*	*Pasteboard right.*
11 workers and 1 ♀ varnished.	3 varnished workers.
2 normal workers, of which one was trying to rub away the varnish of one of its friends.	8 normal workers.

11. At 3 o'clock I replaced the water by esculine and the pasteboard by cobalt.

Result at 3.15

Esculine 1 *cm. left.*	*Cobalt right.*
10½ workers and 1 ♀ varnished.	3½ varnished workers.
8½ normal workers.	1½ normal workers.

One varnished worker and one normal were on the frontier. It is important to note here that each change of the superimposed objects caused a lively anxiety of the normal workers, which began to run, whilst the varnished workers remained impassive. On the other hand, when I lifted the glass which covered the box to change anything inside, the varnished workers quickly recognised the shaking and the fresh air. They then were agitated *quite as much* as the normal ants, and were in no way inferior to them in the agility of their efforts to escape; only when they succeeded in getting away they did not know how to hide like the normal ones.

12. I completely divided the box into two compartments by means of a sheet of pasteboard, leaving sufficient room below to allow the ants to pass. Diffused light.

Then I transposed experiment 11 and replaced the cobalt by 6-8 cm. of water.

Result at 4.30 P.M.

Water 6-8 *cm. left.*	*Esculine* 1 *cm. right.*
9 workers and 1 ♀ varnished.	5 varnished workers.
4 normal workers.	6 normal workers.

The light becoming too feeble, I covered everything with pasteboard.

13. The morning of the following day I found 6 varnished workers and 1 normal on the left, the remainder on the right. I added 5 normal workers. The sky was cloudy. I put the box in my window and at 8 A.M. I placed cobalt and esculine as below.

Result at 9.30 A.M.

Cobalt + 6 *cm. left.*	*Esculine* + 3 *cm. water right.*
3 workers and 1 ♀ varnished.	11 varnished workers.
2 normal workers.	13 normal workers.

14. Preceding experiment transposed at 9.30.

Result at 11.45 A.M.

Esculine + 3 *cm. water left.*	*Cobalt* + 6 *cm. water right.*
8 workers and 1 ♀ varnished.	5 varnished workers.
12 normal workers.	3 normal workers.
1 varnished worker dead.	

15. Without otherwise altering experiment 14, I replaced at 11.45 the esculine by 6 cm. of water and the cobalt by the pasteboard.

Result at 12.25

Water 6 *cm. left.*	*Pasteboard right.*
9 workers and 1 ♀ varnished.	4 varnished workers.
3 normal workers.	12 normal workers.

16. At 12.25, without otherwise changing anything of experiment 15, I removed the water, to add the effect of solar heat to that of light (the sun came out from behind the cloud

a little, but remained dull). The varnished ants had scarcely felt the warmth before they began to run under the pasteboard.

Result at 12.55

Nothing (*glass only*) *left.*	*Pasteboard right.*
0 varnished.	13 workers and 1 ♀ varnished.
2 normal workers sucking the drops of water under the glass.	13 normal workers.

17. Soon after experiment 16, at 1 o'clock, I replaced the pasteboard by the cobalt with water, and I replaced the esculine on the left where there were only 2 normal workers. The ants immediately began to move, partly following a slight shaking of the box. Sun very dull or white clouds.

Result at 1.55

Esculine + 3 *cm. water left.*	*Cobalt* + 6-8 *cm. water right.*
♀ 1 and 4 workers varnished (*sic*).[1]	9 varnished workers.
13 normal workers.	2 normal workers.

One varnished worker was very agitated and ran everywhere, so that his place could not be noted.

18. At 1.55 I simply changed experiment 17. Sun very dull.

Result at 2.35

Cobalt + 6-8 *cm. water left.*	*Esculine* + 3 *cm. water right.*
4 varnished workers (*sic*).	9 workers and 1 ♀ varnished.
3 normal workers.	12 normal workers.
1 varnished worker running all over the place.	

19. Transposition of experiment 18, but during the operation I inadvertently hurt a normal worker, which I removed. Sun very dull, with rain.

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[1] It will be noted that in one or two experiments the author's numbers do not agree. When this is so the fact has been duly noted (see experiments No. 9, 17, and 18).—TRANS.

Result at 3.8

Esculine + 3 *cm. water left.*	*Cobalt* + 6-8 *cm. water right.*
3 varnished workers.	11 workers and 1 ♀ varnished.
11 normal workers.	3 normal workers.

20. Transposition of experiment 19 with great care and without the least disturbance of the ants. Otherwise no change.

Result at 3.13

Cobalt + 6-8 *cm. water left.*	*Esculine* + 3 *cm. water right.*
3 varnished workers.	11 workers and 1 ♀ varnished.
1 normal worker.	13 normal workers.

21. The following morning most of the workers and the ♀ were on the right. During the night all had been covered by pasteboard. To see if, in experiment 16, it was the heat and not the excess of light that made the varnished ants leave the sunny side, I put on the left a red glass without water and on the right 6 cm. of water without anything else, at 8 o'clock in the misty morning.

Result at 9.25, *when a gentle sun had pierced the mists (agreeable heat)*

Red glass without water left.	*Water* 6-8 *cm. right.*
3 varnished workers.	1 ♀ and 10 workers varnished.
12 normal workers. (1 varnished worker lost.)	2 normal workers.

22. At 9.25 I transposed the preceding experiment, since the sun became more and more intense and struck directly on my ants.

Result at 12.30, *with a brilliant, hot sun*

6-8 *cm. water left.*	*Red glass without water right.*
All the 13 workers and 1 ♀ varnished.	0 varnished.
10 normal workers.	4 normal workers squatting in a corner.

The result of the last two experiments, 21 and 22, is very clear. In experiment 21 the normal workers fled from the light, preferring a little more heat. But later, when the heat had become more scorching, they mostly left the red glass to go under the water, preferring the light to such a baking. And then, even, four of them remained under the red glass. The varnished workers were always in the cooler place.

THIRD SERIES

AFTER HAVING TAKEN SOME FRESH *C. LIGNIPERDUS* WITH THEIR LARVÆ AND PUPÆ, I VARNISHED THE EYES OF 11 WORKERS AND 1 ♀. I GAVE THEM A GOOD NUMBER OF LARVÆ AND PUPÆ WHICH WERE IN A HEAP ON THE RIGHT SIDE OF THE BOX, ON ONE SIDE THREE PUPÆ FORSAKEN (DURING THE NIGHT).

23. *Result at* 7.45 A.M.

Pasteboard left.	6-8 *cm. water right.*
3 varnished workers with the 3 forsaken pupæ.	1 ♀ and 8 workers varnished, with all the larvæ and the other pupæ. Several workers were immediately under a little ray from the rising sun. The workers carried the larvæ and pupæ from one corner to the other and remained under the water.

24. I added a normal worker to experiment 23, leaving the remainder unchanged. The light was first diffuse. Then the sun shone on the box. At 1.15 all the larvæ and pupæ had been carried under the pasteboard, where were also all the ants.

25. I then transposed (at 1.15) the preceding experiment after having removed the normal worker, and I left the whole in the sun.

Result at 2.30

6-8 *cm. water left.*	*Pasteboard* 3 *mm. thick right.*
1 or 2 varnished workers under the water.	All the larvæ and all the pupæ had been carried under the pasteboard, where were also nearly all the varnished ants.

Thus the varnished ants carried out the removal alone. It cannot be said that the influence of the sun's heat went for nothing in this result. It is certain that the heat must have been greater under the 6 to 8 cm. of water than beneath the 3 mm. of pasteboard, if we reflect that the sun in summer between 1 and 2 o'clock shone directly on my ants, producing a considerable heat. Several thermometric measurements that I made denoted a difference of about 1° Cent. between the temperature under the water and that under the pasteboard, whilst under the cobalt glass the temperature was raised much more. But this difference is not great, and I am forced to admit that it was the light which caused the varnished workers to effect the removal. This result does not in any way invalidate the preceding ones, for we have here the intense and prolonged action of direct sunlight which must have been perceived through the varnish and which might have a photodermatic action which the mere feeble light had not.

To eliminate as much as possible the calorific factor, I henceforward used the indirect (reflected) daylight entirely, which we will call "diffused light."

26. At 2.50 I transposed the preceding experiment by putting the box in indirect light. The pasteboard was on the left, water on the right. The larvæ and pupæ remained on the right, where they had been. The ants were very active and walked about all over the box, but did not remove the larvæ nor the pupæ.

Result at 3.30

Pasteboard left.	6-8 *cm. water right.*
5 varnished workers.	All the larvæ and pupæ. 6 workers and 1 ♀ varnished.

27. At 3.30 I added a small normal worker at the side of the glass, without changing anything of the preceding experiment. At first it ran everywhere, from side to side, then at the end of four minutes it began to move the larvæ from the water to the pasteboard, although the pasteboard side was quite dry, whereas there was still some damp earth under the water, which the ants always looked for. It moved by itself 8 larvæ in succession under my own eyes. The varnished workers often seized upon

other larvæ, but they only carried them from one side to another of the heap which was under the water. The normal worker was once made to disgorge honey by one of the varnished workers, a fact which showed that the latter were at their ease. I moistened the earth a little on the pasteboard side to equalise matters. By 4 o'clock the normal worker had carried all the 13 larvæ and one small pupa under the pasteboard. It had, on the other hand, left the other pupæ, especially the large female pupæ, on the water side where they had been. I observed one varnished worker bring back towards the pupæ, under the water, one of the larvæ which the normal worker had carried under the pasteboard.

Evening Result

Pasteboard left.	6-8 *cm. water right.*
13 larvæ and 1 small pupa.	Remainder of the pupæ.
7 varnished workers and 1 normal worker.	4 workers and 1 ♀ varnished.

It must be noted that the small workers (minor worker) of *Camponotus* are scarcely able to carry the great female pupæ.

28. At 9 P.M. I added a middle-sized normal worker. Curiously enough the small normal worker then again carried the 13 larvæ and the pupæ under the water. As it was night, both sides were equally dark. Then—

Night Result

Pasteboard left.	6-8 *cm. water right.*
1 or 2 varnished workers.	Almost all the workers, the ♀, the larvæ, and the pupæ.

29. Result of the previous experiment the following morning at 7.30. Diffused light. The normal workers had already removed nearly all under the pasteboard.

Pasteboard left.	6-8 *cm. water right.*
10 larvæ and the great majority of the pupæ.	7 pupæ and 3 larvæ.
4 varnished workers and 2 normal workers.	7 workers and 1 ♀ varnished.

30. Result of the same experiment at 9.45 A.M. Diffused light.

Pasteboard left.	*Plain glass (water removed) right.*
All the larvæ and all the pupæ save one.	One large ♀ pupa.
7 varnished workers and 2 normal workers.	1 varnished ♀ and 4 varnished workers.

We must not forget that resting ants are in the habit of huddling up where their larvæ and pupæ are. When the normal workers had removed the larvæ and pupæ to the pasteboard side, the varnished ♀ and workers had a natural tendency to join them there without any regard for the darkness. One ought not, therefore, to consider the relative frequency of the varnished and normal workers under the pasteboard in the last experiments without taking account of this fact.

FOURTH SERIES

I NOW DIVIDED THE BOX INTO THREE COMPARTMENTS BY PAPER WALLS, LEAVING SPACE FOR THE ANTS TO PASS UNDERNEATH. I THEN PREPARED A FRESH SOLUTION OF ESCULINE WHICH I PLACED THIS TIME IN A PRISMATIC BOTTLE 3.8 CENTIMETRES THICK, WITH PARALLEL WALLS. I CONTINUED TO EXPERIMENT WITH THE SAME VARNISHED AND NORMAL *C. LIGNIPERDUS*.

31. After experiment 30, all the larvæ and pupæ, save one, were on the left. At 10 A.M. I arranged the experiment.

Result at 11 A.M.

Left.	*Centre.*	*Right.*
Cobalt + 6-8 *cm. water.*	6-8 *cm. water.*	*Esculine* 3.8 *cm.*
Several varnished workers.	0	1. All the pupæ (34). 2. All the larvæ (13). 3. The 2 normal workers. 4. The ♀ and one party of the varnished workers.

Within a few minutes of the change made at 10 A.M. I saw the

2 normal workers begin to remove the larvæ from the cobalt to the esculine, passing through the centre compartment without stopping there. The removal was entirely carried out by the 2 normal workers alone. The 11 varnished took no part whatever. They sometimes carried one larva from one corner of the compartment to the other, but without going farther. Once at the end of the removal I saw one varnished worker, evidently fired by the example, carry a small larva from the cobalt to the esculine (as is known, ants do not like to leave one larva alone). This removal of 47 larvæ and pupæ meant considerable work, for it necessitated the medium-sized worker making the most violent efforts to pass the large female pupæ from one compartment to the other under the intermediate band of paper, which scarcely allowed room. The difficulty made the experiment and the contrast between the action of the normal workers and that of the varnished workers all the more striking. At 11 o'clock all had been removed under the esculine.

32. I tried to continue these experiments, but they no longer succeeded. My *Camponotus*, both varnished and normal, seemed overcome by discouragement, which is not rare in like case. They completely abandoned their larvæ and pupæ, and only sought to escape with great violence, without paying any further attention to the light or other stimulus. I then tried with another species.

FIFTH SERIES

FORMICA FUSCA L., NORMAL WORKERS AND FEMALES, IN MY BOX WITH THREE COMPARTMENTS, WITH NUMEROUS PUPÆ WHICH I FIRST PLACED IN THE CENTRE COMPARTMENT, UNDER 6-8 CENTIMETRES OF WATER.

The *Formica fusca* live in meadows and woods, in nests of earth or rotten trunks.

33. Diffused light, at 11 o'clock. The pupæ under the water, in the centre.

Result at 11.30

Cobalt left.	6-8 *cm. water centre.*	*Esculine* 3.8 *cm. right.*
0	0	All the pupæ carried under the esculine.

34. Previous experiment transposed at 11.30. Diffused light.

Result at 1 *o'clock*

Esculine 3.8 *cm. left.*	6 *cm. water centre.*	*Cobalt right.*
All the pupæ had been removed under the esculine.	0	0

35. I added enough ink to the water to make it quite distinctly darker and less transparent than the esculine. Then I transposed experiment 34 as follows at 1 o'clock. Diffused light.

Result at 2.15

Cobalt left.	*Esculine* 3.8 *cm. centre.*	*Blackened water* 6 *cm. right*
0	All the ants had moved with all the pupæ under the esculine.	0

36. Experiment 35 transposed as follows. Diffused light.

Result at 2.45

Cobalt left.	*Blackened water* 6 *cm. centre.*	*Esculine* 3.8 *cm. right.*
0	0	All the ants had moved with all the pupæ under the esculine.

37. Experiment 36 altered as follows at 3 o'clock. Diffused light.

Result at 3.27

Esculine 3.8 *cm. left.*	*Blackened water* 6 *cm. centre.*	*Red glass right.*
0	0	All the workers and the pupæ remained under the red glass.

38. I left experiment 37 as it was, but I replaced the red glass by the cobalt at 3.27. Diffused light.

Result at 3.40

Esculine 3.8 *cm. left.*	*Blackened water* 6 *cm. centre.*	*Cobalt right.*
One party of the ants went immediately with part of the pupæ under the esculine.	o	One party of ants succeeded in hiding with pupæ under a raised paper band and remained under the cobalt.

39. I removed the raised band of paper in experiment 38, but otherwise left things unaltered.

Result at 4.30

Esculine 3.8 *cm. left.*	*Blackened water* 6 *cm. centre.*	*Cobalt right.*
All the pupæ and all the ants were now beneath the esculine.	o	o

40. I removed the esculine of the previous experiment at 4.50.

Result at 5.30

Plain Glass left.	*Blackened water* 6 *cm. centre.*	*Cobalt right.*
o	Nearly all the workers and pupæ were under the blackened water.	Several workers with 2 or 3 pupæ were under the cobalt.

This series of experiments (33 to 40) demonstrates in a manner so clear and so complete the aversion of normal ants for the ultra-violet rays that I considered it useless to continue it. It is a complete confirmation of the results of Lubbock. The heat factor is absolutely eliminated, for if the ants had been too hot they ought to have gone under the water, and if they had been too cold they ought to have gone under the cobalt. The ultra-violet rays alone had for them, it was seen, almost the effect of complete solar light.

Sixth Series

FORMICA FUSCA, WORKER AND FEMALE, WITH EYES AND OCELLI AND PROVIDED WITH PUPÆ. THE VARNISHING OF EYES AND OCELLI WAS VERY DIFFICULT.

41. Four varnished workers with 47 pupæ in the lid of a pasteboard box. I put the pupæ on the side under the glass at 11.30. Diffused light.

Result at 1 *o'clock*

Pasteboard left.	*Plain glass right.*
0	The four workers with all the pupæ remained under the glass.

42. I put the box in the sun, without altering experiment 41.

Result at 2.15

Pasteboard left.	*Plain glass right without water.*
The 4 workers carried 27 pupæ to the shade under the pasteboard, where they themselves remained.	The 20 pupæ which were left remained, somewhat dry, under the plain glass.

43. One series of experiments made with these varnished *F. fusca* and others varnished and normal gave few results owing to the discouragement of the ants, which neglected their pupæ. The total amounts of simple presence of varnished workers are analogous to those of the previous experiments. The varnished workers assembled sometimes under the esculine, sometimes under the cobalt, sometimes under the water, sometimes under the red glass, without appearing to be upset by the light. But certain normal workers were discouraged by doing so much, whereby these results have no great value.

Once, nevertheless, whilst 7 varnished workers and 1 varnished female were settled under the cobalt + 6-8 cm. of water with a very dull sun (direct light), the four most active workers and the female betook themselves beneath the esculine when I removed the water and the cobalt. It is possible that the heat may have acted in this case, but it is also possible that the somewhat strong light may have had something to do with it. I made one or two analogous observations further, but the eyes were found to be incompletely varnished, which made these observations without value. In referring to these cases, I only wish to show how delicate these observations are and how necessary it is to be cautious.

I was more fortunate with a wingless ♀, which, after having been completely varnished with a very dark varnish, busied herself very patiently with the pupæ which I gave her. (The females have, as has been shown by Lubbock, MacCook, and Blockmann, the power of founding new colonies by themselves alone. Their instinct, therefore, makes them, when they are alone, succour the worker pupæ patiently until the time of their hatching. The workers when alone are evidently easily discouraged.)

44. At 1.15, on the 5th of August, my varnished *fusca* female was with the pupæ on the right under plain glass, with a strong diffused light. To the left was the red glass.

At 2.15 the female remained where she was.

At 3 o'clock she had gone under the edge of the red glass.

At 5 o'clock she went afresh under the red glass after transposition.

I replaced the red glass by esculine.

At 5.30 the female was under the esculine.

At 6.0 she was under the plain glass.

August 6th

7.30 A.M. The female was under the esculine by diffused light. I made an alteration by putting 6 cm. of water on the right. The sun came out.

At 9.30 the female had, under the influence of the sun, carried the pupæ from the water to the esculine. Thereupon I returned her to the diffuse light and I made an alteration.

At 1.0 the female remained beneath the water on the right. I made a little disturbance to wake her up.

At 2.7 the female was always under the centre of the water.

At 2.30 she went under the esculine. I made an alteration.

At 2.53 the female remained under the water.

At 3.10 the same.

At 4.0 she had gone under the esculine.

At 4.12 she returned by herself under the water.

At 4.25 under the water.

At 4.42 the same. I put the box on my window to obtain a strong diffused light. Then, towards evening, she walked about between the water and the esculine, now and again taking up a pupa, but not carrying it far.

August 7th

8 A.M. Female under the esculine. Diffused light.

1 P.M. Female under the water. Diffused light.

August 8th

8 A.M. Strong diffused light. The female had heaped nearly all the pupæ under the water, but to the edge of the esculine. I pushed the esculine back a little, so that they were well under the water.

2 P.M. The female had transported a heap of pupæ (apart) under the esculine, but to the edge of the water. I transposed the arrangements, putting the esculine on the left.

A little while after the alteration I saw the female, after a short rest, continue her removal as if I had not made the alteration. Instead of retransporting the several pupæ which she had begun to displace under the place where the esculine now was and where the other pupæ were, she began to search everywhere for scattered pupæ under the esculine to carry them under the water to the heap. The removal was, then, caused not by the light, but by the spirit of order.

At 3.0 the female was under the water, in the centre, with a large heap of pupæ.

At 3.40 the same.

August 9th

2.15 P.M. Since yesterday the female had remained under the water with all the pupæ, despite a strong diffused light, without any alteration having been made in the experiment.

August 10th

10 A.M. The female has remained under the water with the pupæ. I gave her food and drink.

2 P.M. The female had remained with the pupæ to the limit of the water and plain glass, still avoiding the esculine.

August 11th

The female remained under the water (the water is always on the right, the esculine on the left). It may be noted that the esculine was always in a good state of preservation, very florescent.

August 12th

8 A.M. Diffused light. I replaced the esculine by red glass.

At 9.30 the female remained under the water with her heap of pupæ, whilst she had been walking about temporarily under the red glass.

At midday, although I made the sun shine on the box by reflecting it from a glass, the female remained under the water with her pupæ.

August 13th

The female remained all day under the water with her pupæ, by diffused light.

August 14th

7.30 A.M. Always under the water, my female had no inclination to go under the red glass. It might be thought that this was habit, indifference, or discouragement. But this was not so, because when I lifted the plain glass cover of the box, my female *fusca*, frightened, seized the pupæ in great haste and carried them towards the side of the box.

2 P.M. The female had removed the pupæ from the centre to the side of the box, always under the water.

Having wished to again try the effect of the direct sun, I made it act very strongly, which was probably the cause of the death of my female *F. fusca*. I preserved her in my collection. Her eyes and ocelli remain perfectly varnished.

45. On August 7th I varnished the eyes of various *Formica sanguinea* and their *fusca* slaves. I gave them many pupæ in a box with three compartments. At first indifferent, just like various normal workers that I added, they finished by occupying themselves with the pupæ and heaped them up there.

August 10th, the unvarnished ants began to turn their attention to the light. They regularly removed the pupæ from the cobalt and the 6 cm. of water to the esculine. Meanwhile, curiously, it was especially the varnished workers which busied themselves with the pupæ, more than the normal ones.

August 11th, I removed all the normal ants and I arranged, at 8.0, when all the pupæ were on the left.

Result at 10.0

Cobalt left.	6 *cm. water centre.*	3.8 *cm. esculine right.*
All the pupæ remained under the cobalt, in the lightest corner.	0	0

At 10.0 I replaced the cobalt by 6 cm. of water and I opened the box a little to add damp earth. Immediately, after a slight disturbance, the varnished *sanguinea* and *fusca* began to remove the pupæ from the lighted side to the side shaded by the wall (that which was on the side whence came the light). This wall being protected from the sun's rays by a second protecting wall, there was no question of caloric influence. This removal happened under my eyes, with a covered sky (white clouds, a little greyish), but under a direct exposure to daylight. The removal terminated, I returned the box into the reverse position, and the removal recommenced in the reverse direction, *i.e.* the ants carried back the pupæ to the place where they were first, the illuminated becoming the shady side. I twice repeated this arrangement with the same result under a nearly diffuse, but strong light. It should be mentioned that the wall of this box was high, which made the shade very marked. We have in this case very probably to do with a photodermatic sensation. But, curiously, the ants always remained beneath the water, *i.e.* under the light with ultra-violet, and in no way tried to place their pupæ under the esculine, although they often walked about there, and as their comrades that could see had always done the day before. To be more certain, I placed the esculine, which was on the right, in the middle, the pupæ being under the water on the left and even encroaching a little on the centre compartment. When I had turned the box again so as to put them in the light, the ants again removed them towards

the shady side, but under the water, and taking them away from the esculine. They even carried all those pupæ which, encroaching on the middle compartment, were now under the esculine, and transported them under the water on the other side. At 3.30, the light being feeble, the ants ceased to remove, and stayed with the pupæ on the lighted side under the water. Next day I put the box in the other direction, with the esculine in the centre, so as to compel the ants to pass beneath it to reach the shady wall, situated under the water on the right, the pupæ being on the left. They passed under the esculine without stopping there, and transferred all the pupæ from the water on the left to the water on the right. Some *F. sanguinea*, *F. pratensis*, *C. ligniperdus*, and *Lasius niger* with cut antennæ, but not with varnished eyes, put together in the box where my varnished ants had been, immediately after them, began at five or six in the evening, in spite of the very feeble light, to group themselves little by little all under the esculine which remained at the centre, but without worrying about the pupæ. With the onset of night they dispersed again.

Another series of experiments made on varnished *C. ligniperdus* gave me the same results as the first. They did not show any preference for the red glass which I used this time, instead of esculine, in contrast to the cobalt glass. We may dispense with the details.

I have also made a series of experiments with the solar spectrum; with which, indeed, I began. Professors Hofmeister and Weilenmann, of Zurich, were so kind as to lend me their apparatus and to help me to produce a horizontal spectrum. Thanks to the helioscope, I was able, being constantly present, to counterbalance the earth's movement. But in making these experiments, of which the result has been almost completely negative, I have understood why Lubbock's results with the spectrum are relatively little exact. Lubbock used the spectrum of a voltaic arc, which has the advantage of being motionless. To have a very distinct spectrum, one must only take a very narrow band of solar rays. Spread out in the spectrum, this band loses much of its intensity. Then the spectrum itself, in illuminating the box, reflects the rays, which cannot be destroyed in spite of every care, on the surroundings. I make no mention of all the other reflexes to be intercepted. We may add that, in order to experiment, a spectrum must be sufficiently large, which diminishes its intensity, and that, in spite of the helioscope, the terrestrial movement is very troublesome.

Briefly, the *Lasius niger* and the *Formica fusca* with numerous pupæ, on which I made the spectrum shine, paid very little attention to it. It is true that I observed several removals from the ultra-violet and from the violet to the red, but I also saw some in the opposite direction. I did not even try to varnish the eyes of these ants, the normals not having shown a distinct reaction. Perhaps this result may be in part owing to my working in the autumn, a period when the ants become generally indifferent.

I think I can recapitulate in two words the result of the above experiments. 1. *The ants perceived the light and particularly the ultra-violet, as has been shown by Lubbock.* 2. *They appeared to perceive the ultra-violet principally with their eyes,* i.e. *that they see it, because when their eyes are varnished they appear almost indifferent; they react, then, distinctly only with a direct or at least strong sunlight.* 3. *The experiments seem to indicate that the photodermatic sensations are more feeble in ants than in the animals studied by Graber.*

It is clear that these questions yet call for numerous investigations. It might be thought, and this appears to me sufficiently plausible, that the photodermatic sensations are specially of service to animals which are nocturnal, subterranean, or live in dark waters. They would help them to avoid, in a general way, the light, and would become more and more useless, the more the animals are diurnal, when they possess eyes. It is true that a more or less large number of animals see the ultra-violet; nocturnal animals have as much reason to avoid it as to avoid the other rays. The strong chemical action of the ultra-violet seems to make it particularly apt to affect the nervous system. And it is probable that if it affects our retina so little, it is simply because, as Soret has shown, the refracting media of the vertebrate eye absorbs it in very large part.

The facts and the reflections which proceed made me curious to know whether man has not photodermatic sensations. I consulted an ophthalmologist, who could only point out to me an assertion of Schmidt-Rimpler, according to which the blind know if they are in a *light* and airy place (hell luftig) or in a *dark* and narrow room. I have questioned a blind person on this subject, and he has assured me that he was incapable of distinguishing a light room from a dark one. I begged him to submit himself to some experiments, which he did with pleasure. I made him pass from light rooms to rooms completely darkened. I have been astonished in making these experiments at the delicacy with which he appreciated the least air, the least difference of temperature which I did not appreciate, and especially how he at once judged of the dimensions of a room by the sound of the voice and footsteps, perhaps also by the movements of the air. On the other hand, from the point of view of the light, when I took care to eliminate the factors of sound, temperature, and air, he displayed the most complete ineptitude. He was forced to "guess" if the room where he found himself was light or dark, but he regularly guessed wrong. This observation scarcely speaks in favour of photodermatic sensations in man. But further research would be necessary in this direction. Nevertheless, the fact that the blind person was not conscious of like sensations does not absolutely prove that the photodermatic irritations do not reach some ganglionic or even subcortical centre.

Ants do not fear the light as a general rule. They only fear it at rest, or for their larvæ or pupæ. In his researches on marine animals, Graber found several species which love the light and avoid the darkness (as the red starfish, *Asteracanthion rubens* Retz.). A large number of them prefer blue and violet to red light. Some appear even to prefer the ultra-violet to other rays, but this point is not very explicit in Graber's work.[1]

To return again to the important question of heat. I believe that experiments 30 to 40 and several others are perfectly clear on this subject. As all these experiments were made in summer, with great heat, the ants fled from the strongest heat and always sought the more feeble. Supposing even that the slight differences of radiant heat by an exposure to the diffused light between the cobalt, the 3 cm. of esculine and the 6 cm. of blackened water could influence them, they ought to go under the blackened water which intercepted the heat most. Then the fact that the red glass (without water), which let most of the heat pass, produced on the ants the same effect as the solution of esculine, which intercepts heat much more than the cobalt, shows without any doubt that it is the light and not the heat which influenced our ants. Finally, the fact that the varnished ants less often showed themselves refractory to the influences of the light, whilst they reacted very well to differences of temperature, proves that it is rather the light and not the heat that influenced the normal ants.

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[1] Reference may be made here to experiments made by Lubbock with the spectrum on *Daphnia*, in which that observer thought to have shown that they distinguish between rays of different wave lengths, and "prefer those which to our eyes appear green and yellow." Vide *Senses of Animals*, 1888, page 211 *et seq.*—Trans.

What are we to think now of the photodermatic sensations? Can we compare them to vision? At all events they can only give a general sensation of light and colour, without form or anything like it. But it has not even been shown that these sensations have a special energy which can be rightly called optical. All that Graber has shown reduces itself, as in his experiments on what he took for smell in insects, to the fact that light is perceived in a very general way, sometimes less painfully and more agreeably from the red end, and more painfully and less agreeably from the violet (photophobic animals), sometimes in exactly reverse proportion (photophilic animals). Graber has in no way shown that the sensations produced by light on the skin have a particular, special quality, different from sensations of pain, of heat, of cold, or of touch. He has not demonstrated that the animal can with their help recognise any object; that it distinguishes a blue object from a red object, for example. The quality of the sensations might well be bordering on our sensations of cold and heat, and entirely different from our optical sensations. This appears to me the most probable. Also I prefer, for my part, rather the term *photodermatic* sensations, the term also employed by Graber, to the term *dermatoptic* sensations, which, in my opinion, says too much. In a word, the animal does not "see" by the skin; it only feels the light, its degrees and the length of its waves.

I describe, in the form of appendix, an observation made on my *Camponotus ligniperdus.* I had taken these insects in their nest and had established them in a bowl. Forty-one days later I turned out the contents of the bowl at the edge of a wood, close to a hole made to give refuge to both varnished and normal ants, and I took a second part of the nest with larvæ, pupæ, and many more workers than on the first occasion. As I had too many inhabitants for the bowl, I turned out half of them by the side of the old ones, towards the hole, at the edge of the wood. I thought that, as usually happens, the ants would quickly recognise them. Instead of that, very lively individual struggles occurred, which I have called, in my *Fourmis de la Suisse*, "fights in cold blood." The new ants showed at first a great mistrust when they met an old one, and vice versâ. They drew back this way and that, menacing with their mandibles, thoroughly examining with the antennæ, even biting. Several even went in their irritation so far as to try to decapitate and even to decapitate several of their old friends and sisters with their mandibles (which is the method of fighting with *Camponotus*)! The varnished ants took part in these affrays as well as the unvarnished ones; I even saw them attack, and they were scarcely less adroit. The fights did not entirely cease until the end of one or two days, and apart from the several victims of the first day, the incident was terminated by an alliance. Eight days later, I added to the ants' nest the remainder of the new *Camponotus* which I had kept in the bowl for my experiments and which comprised a good number of new varnished ants. This time there was not any dispute. The ants quickly recognised each other. It was not then "the smell of the bowl" which, in changing the primitive odour of the ant-hill, had caused the enmity. But in the first case the separation had lasted forty-one days, in the second case only eight.

This observation thoroughly confirms what I have said elsewhere (*Bulletin de la Soc. vaud. des sciences naturelles*, xx. 91, 1885, p. 7, and *Fourmis de la Suisse*). It is impossible to make a rule for the faculty of recognition among ants; even individual differences may be observed, and outside circumstances go far to determine hostile or amicable meetings, war or alliance. A common critical situation between two parties, the sudden mingling, easily provokes an alliance among the same ants which fight each other almost to complete extermination of one colony at least, if they meet under normal conditions. But this fact confirms, as I have said, the great differences among species, and especially among the different genera of ants. I had not then experimented on this point with *Camponotus ligniperdus*, which appear thus to have short memories and quickly forget their old brethren. The above facts show further that I was plainly right (*Fourmis de la Suisse*) in considering the play of antennæ and the reciprocal examinations of ants which meet again after long separation as the signs of fear and distrust and not as evidences of joy and affection, as Huber believed. I add that at the time when this fight between sisters took place, no working pupa of the year was yet hatched. The combatants had then all been living to the adult state under the same roof, like sisters, six weeks before, whilst Lubbock observed ants which recognised each other after more than a year of separation.

Lubbock (*l.c.*) thought to show that ants removed from their nest in the pupal state and hatched away from home were nevertheless recognised by their companions when they met them. In my *Fourmis de la Suisse* I thought I had shown the opposite. Here is an experiment which I made in those days: August 7th. I gave some pupæ of *Formica pratensis* near hatching to several *Formica sanguinea* in a box. On August 9th, some hatched. On August 11th, in the morning, I took one of the young *pratensis*, aged two or three days only, and carried it to the ant-heap of its birth, which it had left as a pupa only four days previously. It was very badly received there. Its nurses of four days ago seized it, one by the head, one by the thorax, one by the feet, recurving their abdomina with a menacing air. Two among them pulled it a long time in the opposite direction, each by a foot, as if tearing it to pieces. Nevertheless they ended finally by tolerating it, as was done also for other ants of the same age (still yellowish-white) coming from different ant-hills. I waited two days further to let my newly hatched ants harden a little. Then I replaced two in their nest. They were violently attacked.

One of them was overwhelmed by venom, pulled about and killed. The other was pulled about a long time and bitten, but finally left quietly (tolerated). The odour of the *sanguinea*, which had lived four days with the first and six days with the last two, may be considered as an objection. To that I will simply reply by the experiment on pages 278 to 282 of my *Fourmis de la Suisse*, where some adult *F. pratensis* separated *two months* from their companions by a forced alliance with *F. sanguinea*, an alliance which I had caused, immediately recognised their old friends and went among them almost without dispute. I therefore maintain my opinion: ants learn to know each other little by little after their hatching. I believe further that this is by means of olfactory and touch perceptions.

I may be permitted in conclusion to offer to Professor L. Soret my most lively thanks for his help, which was as obliging as efficient.

NOTE TO CHAPTER IV

FRONTAL OCELLI.—One final word as to the frontal ocelli: after mature reflection, I have come to the conclusion that they probably are of use to insects which have otherwise good vision, to distinguish light in relatively obscure surroundings and also movements in their immediate neighbourhood. We have, as a matter of fact, seen that insects with relatively distinct vision have the crystalline very long and very narrow. This causes a great loss of light and necessitates a strong light, as Plateau has pointed out. Therefore insects with distinct vision need more light than those with indistinct vision which have short crystallines. But we see frontal ocelli present in insects which need, on the one hand, a distinct vision, because they partly lead an aerial existence; and, on the other, need to move in semi-darkness, because they inhabit more or less dark nests. This is the case with bees, wasps, male and female ants. But among worker ants the ocelli become for the most part of the time superfluous, because their compound eyes become flat (short crystallines). Nevertheless we see the ocelli present in worker ants with distinct sight which have more developed eyes, as in *Gigantiops*, *Polyergus*, and *Pseudomyrma*. It is clear that, even on this hypothesis, the rôle of the ocelli remains a very humble one, for on earth in the semi-darkness it is the antennary sense which assumes the part of chief guide. Most aerial insects do not have ocelli, because they do not require this double adaptation to a strong light, and at the same time to a feeble light on or under the ground. In nocturnal insects the facets are adapted to night vision.

CHAPTER V

INSTINCT OF DIRECTION—SMELL—TASTE

Instinct of Direction

M. J. H. FABRE (*Souvenirs Entomologiques*, 1879) has made some very ingenious experiments concerning what he calls the instinct of direction. After having marked some *Chalicodoma* and other social hymenoptera, he shut them in a box, and making several detours, carried them to three and even four kilometres' distance. Then he released them. Despite the distance, the insects, after raising themselves to a certain height, flew in great part directly in the direction of their nest, where they were found, on his return, at the end of a quarter of an hour to an hour. Nevertheless a good number of them did not return. M. Fabre appears to me to have neglected the importance of this latter point. Instead of attributing these facts to an instinct of direction, I base my opinion on the results of the first part of the present work, and I explain them as follows: Aerial insects and aerial beings in general, soaring above terrestrial objects, ought to have, and have, a knowledge of places very different to that of wingless beings, much more compendious and much more extended. Terrestrial beings see their horizon continually obstructed, which makes their direction by sight much more difficult. If we reflect on the geographical *coup d'œil* "as the crow flies" that one obtains on the summit of a hillock, we shall have a feeble idea of what the vision of the aerial being can be, with this difference, that in a twinkling of an eye it moves and alters its horizons, which we cannot do. In twenty minutes the *Chalicodoma* of M. Fabre had travelled over their three kilometres! The experiment of M. Fabre simply proves to me the very instructive and very interesting fact that the *Chalicodoma* knew the places within a radius of a league, at any rate. Those which did not find their way were probably newly hatched and had not pushed their reconnaissances so far. What strengthens me in this conviction is that the worker ants, though wingless, likewise know the places and the direction for several metres around their nest. But a league for an aerial insect as large as a *Chalicodoma* is certainly no more than four metres for a poor wingless ant. The proof is that the *Chalicodoma* got over his three kilometres in twenty minutes, and that the ant (when isolated) needs an equal time to cover several metres.[1]

Smell or Antennal Sense

So much has been written on the sense of smell in insects that it is almost gilding refined gold to return to this subject. I have, however, two reasons for so doing: on the one hand I wish to relate here several experiments which I have made on this point; on the other a new work by Graber,[2] although extending our knowledge by a large number of experiments and by various new facts, is likely to cause a certain confusion in the subject which occupies us.

What is understood by smell in the lower animals? I return to what I said at the very outset of these experiments, and I believe that we can define this sense in the following way:—

A special sense which allows the animal to recognise at a distance by some specialised energy the (*chemical*) *nature of a certain body.* To demonstrate the sense of smell, our two physical distance senses, vision and hearing, must first be eliminated with certainty. But that is not sufficient. Innumerable chemical substances included either in air or in water in the state of gas (free or absorbed) can, as is known, and as I have already pointed out at the commencement of these experiments (1878), while exercising in any way some corrosive action, irritate nerve terminations other than those of olfaction, and that (at least as far as concerns man) generally in a painful or at least disagreeable fashion. This is especially the case with the mucous membranes, of the ocular conjunctiva in particular.

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[1] This matter is treated at much greater length in a later Chapter.—TRANS.

[2] V. Graber, *Vergleichende Grundersuche über die Wirkung und die Aufnahmestellen chemischer Reize bei den Thieren.* Biologisches Centralblatt, Sept. 1, 1885.

When a little ammonia, benzine, chloroform, vinegar, or sulphurous acid is brought near to the eye, a painful irritation of the conjunctiva is felt which has no connection with smell. But while we appreciate the smell of benzine, for example, at a considerable distance, it is necessary to bring this liquid very close to the eye for the conjunctiva to be affected. In general it may be said that for such irritation to be produced it is necessary that the irritant substance should be relatively concentrated or brought very close. Olfaction, on the contrary, is a reaction, infinitely more fine, that can perceive substances at great distances, even diluted almost to infinity (as the smell of musk for man). We know that a certain pathological condition of hyperexcitability of the brain, hyperæsthesia, allows us to perceive agents which we cannot ordinarily perceive, or to perceive those which we already recognise in a more dilute condition than normal. This is specially true for the simple painful tactile irritations (not olfactory) of which we have just spoken. But it is not only by the degree of intensity, of delicacy, of the perception, it is above all by its quality, by its "special energy" that olfaction is distinguished from other irritations produced by gaseous vapours or by liquid solutions on certain mucous membranes. Now this special energy, which allows us to distinguish a hundred different odours one from another, we know well by our own sensations, but how can it be shown in others! If we are content, as our predecessors have so often been, and as Graber is again, to bring close to an animal certain substances which are odorous to us, and see whether or not it avoids them, we have not demonstrated olfaction at all. We have simply shown that these substances have irritated the animal in one way or another. If the animal comes up to them instead of avoiding them, we have the proof that the irritation is agreeable to it. That nearly approaches olfaction, but is by no means a proof of it, for certain irritations of the skin can be agreeable without, for all that, being olfactive. It is necessary, then, as I have said, to show that the irritation in question allows the animal to recognise such or such matter, to distinguish it from others in a constant and indubitable fashion. Then we have the right to speak of olfaction, and it is even in my opinion the only proof, the only definition of this sense that we have. If I show, for example, that a blinded dog which has been shut up in a case and carried to a distance nevertheless finds its way back and quickly returns to the point of departure, I shall have the proof that this dog smelt and recognised his track. This observation could easily be made still more decisive. It would suffice, after having repeated it several times (changing the locality), to remove the olfactory bulbs of the dog. I do not know if this experiment has been done, but I am sure that he would no longer find his way.

If I show that a male *Saturnia*, which lives in the woods or at least in the country, starts looking for a female hatched in my room in the centre of a town, that it comes—as it were—knocking at my closed window to try and enter my room; if this is not one male, but quite a swarm of males of *Saturnia carpini* which comes thus besieging my window, I have good right to believe that I have shown in these insects a special sense which corresponds to our olfaction. This observation I made at Lausanne on *Saturnia carpini*, of which I had reared a certain number in my room. The swarm of males which came outside, after the hatching of my females, to besiege my window, was such that it caused a crowd of ragamuffins in the street. These urchins sought to catch these beautiful butterflies, and they could not get over their surprise at seeing them knock at my window and enter my room when I opened. Entirely analogous observations have, further, been made by other authors long before me.

If I show further that the loss of an organ constantly involves the loss of this faculty of recognition, I shall have shown that this organ is the special organ of olfaction, as we have defined it, and that even though the animals deprived of this organ continue to react to painful chemical stimuli or even to certain agreeable stimuli.

We have said above that a special cerebral lobe corresponds to olfaction, as to vision, which, in insects as in vertebrates, occupies the most interior portion of the brain, and from which comes a large special nerve, the olfactory or antennal nerve. Great as our prudence ought to be in making morphological homologies among beings so diverse, I feel I must insist upon the fact that the olfactory lobe and bulb are the most constant sensory centres, both in their position or morphological localisation and by their structure, throughout the series of vertebrates, even in the lowest forms.

It is particularly to be noted that olfaction maintains, even in the lowest forms, its connections *sui generis* with these two specialised cerebral organs: the olfactory bulb and the olfactory lobe. But as vertebrates spring from the worms or the ascidians, the homology appears to me to remain the same. This fact, without being an absolute proof, has a decided value and should not be neglected. The more the sense of smell is developed in a vertebrate, the larger the olfactory bulb and lobe. Man is, of all the vertebrates, save the cetaceans, perhaps, the one in whom the olfactory lobe and bulb are relatively the most rudimentary. We can evidently, therefore, form only a feeble idea of the world of knowledge, of representations, that the olfactory perceptions impart, for example to a dog, to a mole, or to a hedgehog, animals in which the olfactory bulb and lobe constitute one of the largest parts of the brain.

Then comes a fundamental fact to which Graber does justice, although his whole system of experimentation begins by not taking it into account. We have the bad habit of calling odoriferous substances (*Riechstoffe*) the substances which are odoriferous for us. But the study of all animals very quickly shows us that the differences between the animal species are enormous, that a substance may be extremely odorous for one species and not so for another and vice versâ. The dog, whose sense of smell is of an extreme delicacy for certain tracks that we are incapable of perceiving, is insensible to the scents which affect us in the highest degree, etc., etc. It is very quickly observed in insects that the faculty of perceiving certain emanations is intimately allied to their course of life, to their wants and to dangers which they have to avoid. The female of each species is odorous to her male. A plant that attracts a certain insect from very far off leaves others indifferent and is absolutely inodorous to us, etc.

Graber's system of experimentation is as simple as it is monotonous. He applies the system of his experimentation on photodermatic sensations (of which the method is similar to that of Lubbock) to the investigation of olfaction. He places various insects in the centre of a box divided into two compartments which communicate below. Above one of them he places an odorous substance, and observes at the end of a certain time in which of the two compartments the insects are specially gathered together. He gives the amounts and infers olfaction when the greatest number of insects regularly assemble, whether under the odorous compartment or under the other. Graber has especially employed substances with strong, often corrosive, emanations, always strong odours. In many cases he finds that insects deprived of their antennæ behave like those which have their antennæ. But it is not always so, Graber acknowledges himself, for *Aphodius*, for example, which gathered in mass under cow dung, ceased to do so when he cut off their antennæ. Here Graber had really chosen an object sought for by the insect in the natural state. He likewise ends by admitting that a certain olfaction truly resides in the antennæ. But let us examine a little some of Graber's other experiments which appear convincing.

Graber put some *Lucilia Cæsar* (golden flies) in his box, and found finally that 169 had been under the compartment where decomposing food was to be found, whilst only 92 had gone under the other. Then he removed the antennæ and found that 101 had been under the food and only 39 on the other side. He thinks he has proved irrefutably thereby that they recognised the food without antennæ. I beg to reply:—

1. That the numbers in both cases are too little different to prove much.

2. That rotten food shut in a box is a reagent of such violence that it is very possible that it caused tactile or gustatory sensations in these insects without the sense of smell, properly speaking, coming into play.

3. Finally and especially, flies shut up in a box are so far from their natural state, so frightened and out of place, that the result is not at all astonishing. But I call the result obtained by the flies provided with their antennæ (proportion 169 to 92) an almost negative result.

Let us take the *Formica rufa*. Graber found that it did not like essence of rose, and I believe this, for ants do not look for roses. He found that 515 ants had been in the empty compartment and only 42 in the one containing the essence. Then he used ants deprived of antennæ and found that 165 were under the essence and 299 on the other side. It seems to me that this result is scarcely sufficient to *prove* that the ants have an organ of smell other than the antennæ. Similar figures could show the contrary of what Graber assumes almost as well. By even admitting the possibility that the essence of rose thus shut up had a little disagreeably impressed the mouth or palpi of the ants without antennæ, Graber *has not absolutely proved that ants with or without antennæ may be in a state to recognise the essence of rose as such, to distinguish it from another substance, to find it when it is hidden.* Nevertheless Graber appears to be in the main of my opinion, and reading page 454 of his work, for example, I cannot understand how he continues to talk of smell and of odorous substances for all his experiments, for he himself recognises at this strait that the question is that of perceptions analogous to those of the conjunctiva of our eye, and that the animal has further need of *distinguishing*, of *recognising* its sensations one from another to make them useful.

Graber found that *F. rufa* went in numbers into the compartment where was a flower, the *Philadelphus coronarius.* This fact probably is approached to a true smell. It would be interesting to see if they do so also when they are deprived of their antennæ, which Graber does not tell us. Ants pillage the nectar from various flowers, hence the fact is not astonishing.

The fact that appeared as the result of the experiments of Graber is that a large number of substances with penetrating emanations or with strong odour for us affect insects generally in a disagreeable manner, or that these impressions often persist when the antennæ are removed, principally when it is a question of substances with a very penetrating odour, as turpentine, butyric acid, essence of rosemary. Whereas essence of rosemary very quickly causes a reaction with *Silpha thoracica,* even when it is deprived of its antennæ, assafœtida does not cause any. When the insect has its antennæ the reaction due to assafœtida is as rapid as that due to essence of rosemary.

Now let us recall several fundamental experiments by Graber's predecessors.

Alex. Lefebvre[1] showed by an experiment, as careful as judicious, that a bee occupied in eating sugar did not notice a needle wetted with ether until it was brought near to its head, and it was the antennæ that were turned towards the needle. When he approached the needle to the abdomen, to the stigmata, even touching them, the bee did not react at all, some little care being taken to come from behind, under the abdomen, to avoid the antennæ (and the eyes). He found that wasps from whom he had removed the antennæ were not sensible of the ether.

Perris,[2] in his excellent memoir on the seat of the sense of smell in the articulata, showed clearly that the experience of every entomologist who had himself observed the habits of insects with discernment should convince him of the fact that the sense of smell in these animals resided in the antennæ. He showed that *Cynips*, *Leucospis*, *Bembex* recognised by the aid of their antennæ their prey hidden underground or in the wood. He bewildered some *Dinetus* by passing his hand over the place where they had hidden their egg and their prey, or by intercepting the emanations of this latter by means of a square of paper hidden under ground, etc. Then he repeated experiments analogous to those of Lefebvre with the same result. Perris assigned to the palpi a feeble olfaction at short range. He pointed out that the araneida, the only articulates which have no antennæ, appear to have quite rudimentary sense of smell.

I add briefly that the following authors have further pleaded the cause of olfaction by the antennæ :—

Roesel,[3] De Blainville,[4] Robineau Desvoidy,[5] Erichson,[6] A.

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[1] A. Lefebvre, *Note sur le sentiment olfactif des antennes.* Annales de la Société entomologique de France, 4 juillet 1838.

[2] Ed. Perris, *Mémoire sur le siège de l'odorat dans les Articulés.* Actes de la Société Linnéenne de Bordeaux, t. xvi. 3me et 4me livraison, 1850.

[3] Roesel, *Insectenbelustigungen.*

[4] De Blainville, *Principes d'anatomie comparée*, i. p. 339.

[5] Robineau Desvoidy, *Recherches sur l'organisation vertébrale des crustacés et des insectes.*

[6] Erichson, *De fabrica et usu antennarum in insectis.* Berlin bui Unger, 1847.

Dugés,[1] H. Kuster,[2] Slater,[3] Vogt,[4] Dönhoff,[5] Cornalia,[6] Hauser,[7] Kraepelin,[8] Lubbock,[9] Schiemenz,[10] and myself.[11] I particularly recommend the very remarkable work of Kraepelin, who includes a very complete and very clear critical review of all the preceding works, as well as excellent anatomical descriptions with plates.

Rosenthal[12] believed he had found the organ of smell in a membrane stretched between the two antennæ of diptera.

Kirby and Spence,[13] Wolff,[14] and Graber[15] believed that they recognised it in the terminal nervous apparatus of the palate (back of the pharynx) of certain insects.

Treviranus (after Carus, *Vergleichende Anatomie*, Bd. i.) sought the sense of smell in the œsophagus.

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[1] A. Dugés, *Traité de physiologie comparée.* Montpellier et Paris, 1838, vol. vii. p. 161.

[2] Kuster, *Zoologische Notizen.* Isis von Oken, 1844, col. 647-655 (cited by Plateau).

[3] Slater, *Ueber die Functionen der Antennen b. d. Insecten.* Froriep's Notizen, 1848, iii. No. 155, p. 68.

[4] C. Vogt, *Zoologische Briefe*, vol. i. p. 516.

[5] Dönhoff, *Bienenzeitung*, 1854, p. 231, and 1851, p. 44.

[6] Cornalia, *Monografia del Bombice del gelso.* Mem. d. R. istit lombardo di scienze, vi. pp. 304-305. Milano, 1856.

[7] Hauser, *Physiologische und histol. Untersuchungen üb. d. Geruchsorgan der Insecten.* Zeitschr. f. Wiss. Zoologie, xxxiv., 1880; and Bull. de la Soc. des amis des sc. nat. de Rouen, 1881.

[8] Kraepelin, *Ueber die Geruchsorgane der Gliederthiere.* Osterprogr. d. Realschule des Johanneums, p. 25. Hamburg, 1883.

[9] Lubbock, *Ants, Bees, and Wasps.* London, 1882.

[10] Schiemenz, *Ueber das Vorkommen des Futtersaftes, etc., der Biene. Dissertation der Univ.* Leipzig, 1883 (bei Engelmann).

[11] A. Forel, *Les fourmis de la Suisse*, p. 119. Genève, en commission chez H. Georg, 1874. *Ibid.*, Zeitschrift f. Wiss. Zoologie, xxx. Supplément, p. 61, 1878. *Ibid.*, *Beitr. z. Kennt. d. Sinnesempf. d. Insecten.* Mitth. d. Münchener entom. Vereins, 1878, p. 18. *Ibid.*, *Ét. myrmecol.* en 1884. Bull. Soc. vaudoise des sc. nat., xx. No. 91, p. 334, Feb. 1885.

[12] Rosenthal, *Reils Archiv für Physiologie*, t. x. p. 427.

[13] Kirby and Spence, *Introduction to Entomology*, t. iv. p. 263, and t. iii. p. 454.

[14] O. J. B. Wolff, *Das Riechorgan der Biene.* Nova acta d. K. L. Car deutsch. Akad. p. Naturf., Bd. xxxviii. No. 1, 1875.

[15] Graber, *Naturkräfte*, Bd. xxi. Insecten, Theil i. p. 304. It is curious to see Graber in this work turn to ridicule the idea of an olfactory perception in the antennæ, and laud Wolff to the skies. In his last work, where his opinions are much changed, he no longer quotes this old work!

Baster,[1] Lehmann,[2] Cuvier,[3] Duméril,[4] Burmeister,[5] Joseph[6] thought it should be placed in the stigmata or the tracheæ. Joseph thought he found nerve terminal organs in the stigmata, but his preparations were insufficient, as I have been able to assure myself, as also were those of others, and nothing of the kind has been verified.

Bonnsdorf,[7] Marcel de Serres,[8] and Knoch[9] consider the palpi (Knoch the maxillary palpi only) as organs of smell.

Finally Perris (*l.c.*) and Comparetti[10] believed that the palpi served for olfaction near the antennæ. Comparetti placed smell, however (as Graber appears to have done in his last work), in different organs according to families: antennary clubs of lamellicorns, proboscis of lepidoptera, forehead of orthoptera.

Before going further in this maze of opinions, I may be permitted to here recapitulate some experiments which I have published here and there.

1. Aug. Forel, *Fourmis de la Suisse*, 1874, p. 119.

"I put together in the same bowl ants of species and even of genera entirely different (*Camponotus ligniperdus*, *Tapinoma erraticum*, various species of *Lasius* and *Formica*), after having removed both antennæ in all. They mingled thoroughly, without distinction; I saw some *Lasius* lick some *Formica* and some *Camponotus*; I even observed a commencement of disgorging between a worker *Lasius fuliginosus* and a worker *C. ligniperdus.* These ants only perceived the presence of honey when their mouth happened to dip into it by accident; they then began to eat it, but clumsily, and they always finished by soiling their front feet (with which they sought to feel in place of their antennæ). These ants let it be seen clearly that their intelligence had not suffered at all, but that they were no longer capable of delicate sensations. They tried as much as possible to orient themselves with their feet, their palpi, and their head, making these organs perform unaccustomed movements. When they met one another, they felt with their palpi and their front feet, and evidently ended, as we have seen, by taking each other for friends. I saw, nevertheless, on several occasions, certain well-marked gestures of mistrust, such as a sudden recoil with menaces of the mandibles, but nothing came of it."

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[1] Baster in Lehmann, *De sensibus externis animalium exsanguinum, insectorum scilic. ac vermium, commentatio.* Goettingue, 1798.

[2] Lehmann, *De usu antennarum*, p. 27.

[3] Cuvier, *Leçon d'anatomie comparée*, t. ii. p. 675.

[4] Duméril, *Considérations générales sur les insectes*, p. 25.

[5] Burmeister, *Handbuch der Entomologie*, T. i. pp. 196 and 277.

[6] Joseph (G.), *Tageblatt der* 50. *deutschen Naturf.-Versammlung in München*, 1877.

[7] Bonnsdorf, *Fabrica, usus et differentiæ palparum in insectis. Dissertatio.* Aboae, 1872.

[8] Marcel de Serres, *De l'odorat et des organes qui paraissent en être le siège chez les orthoptères.* Annales du Muséum, xvii., 1811.

[9] Knoch, *Dans Lehmann, De sensibus externis, etc.*

[10] Comparetti, *Dinamica animale degli insetti*, ii. p. 442. Padoue, 1800.

"On another occasion I put some *F. fusca* workers from the same nest, and from which I had removed the antennæ, in a bowl with their larvæ, their cocoons, and some earth. They did not even attempt to dig in the least, nor take the least care of their larvæ, which soon perished. They remained thus inactive during a fortnight, motionless most of the time, presenting the most sorry aspect. I had put with them a *F. pressilabris* worker, also deprived of antennæ. They did not do him any harm."

An exactly parallel experiment in which I had removed the front feet of some *F. fusca* above the spur had a different result. They quickly killed a *F. pressilabris* that I gave them (and later the one I had given to their antennaless companions when I had reunited the two groups). They made every effort to dig and to build dwellings, but in vain. They soiled themselves all over without succeeding in their endeavours (they no longer had their spurs to clean their mouths, etc.). They attempted to look after their larvæ, but dirtied them completely. They thus finished by perishing, for their instrument and their principal *point d'appui* (apart from their mandibles) failed them.[1]

2. Aug. Forel, *Zeitschrift f. Wissensch. Zoologie*, Bd. xxx. Suppl. 1878, p. 61.

(I have made a rather free translation from the German.)

"The physiological deductions of Wolff (*l.c.*) are in my opinion in great part as unhappy as his purely anatomical researches are conscientious and important. He found behind the labrum, in the dorsal membraneous part of the palate, a terminal nerve organ which he believed to be the olfactory organ, and the mandibular glands of the two sides of the head (already described by Meinert[1]), which he called olfactory mucous glands (*Riechschleimdrusen*), and of which the secretion according to him serves to moisten the olfactory organ.

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[1] I reunited them to their companions which had been deprived of antennæ. The two groups of cripples did not know how to help one another, like the blind man and the paralytic in the fable.

"He attributed chemical properties to this secretion (decomposition in the air, etc.), by the help of which he thought to throw a great light on the physiology of smell, even in vertebrates and man.

"Wolff should have begun by making sure by means of experiments if his organ was truly olfactory, instead of seeking proofs in the incomplete experiments of authors belonging to the commencement of our century[2] (those of F. Huber). Furthermore, if he had reflected with an unbiased mind on the results of his own researches in comparative anatomy, he must necessarily have recognised his error. Indeed, he found the olfactory organ most developed in the queen bee, then came the worker bees, then a whole series of other hymenoptera where he found his organ more and more ill-developed, finally consisting of a pair of nerve terminations only in certain braconides and disappearing entirely in others. But the braconides must necessarily have a very delicate sense of smell to discover, in order to lay their eggs there, victims often deeply hidden by their parents, whilst Lubbock (*Obs. Ants, Bees, and Wasps*; Linn. Soc. Journ. Zoology, vol. xii.) has clearly and irrefutably shown by very ingenious experiments that hive-bees have a bad sense of smell. But Wolff reasoned as follows: 'The nervous organ of the pharynx is rudimentary in the braconides; therefore the braconides have a detestable sense of smell!'"

"I may be allowed to mention here two simple little experiments which I repeated on June 22nd, 1876, in the presence of the Société de morphologie et de physiologie of Munich, and which the members there present have found very conclusive."

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[1] Meinert, *Bidrag til de danske Myrers Naturhistorie*; in kgl. danske Videnskabernes Selskabs Skrifter, 5. Raekke, nat. og. mat. Afd. v. Bind., 1860.

[2] The nineteenth century.—TRANS.

"1. After having made three *Pollistes gallicus* (species of wasp) fast a little, I removed both antennæ in the first; then in the second the whole of the front of the head to the eyes, and, further, all that remained of the pharynx after having drawn it out from the surface of section; the third I left intact. After a short rest I plunged the head of a pin in honey and I brought it to the wasps, which were quiet. It was necessary to approach it to about 1 cm. to attract the attention of the normal wasp from rest. But when it had smelt the honey it directed both antennæ, quivering them, towards the pin. If the pin was withdrawn slowly without letting it touch the wasp and without removing it too far, one saw the insect follow it and lick up the honey when it touched it. The wasp from which I had cut away the front of the head, and consequently removed all the sensory organs of the mouth, including the organ of Wolff (which it is easy to dissect in the extirpated pharynx), behaved exactly like the normal wasp. It smelt the honey as far as the latter, directed its antennæ towards the pin and pursued it in the same way. When allowed to touch the honey, it tried to eat, naturally in vain, having no longer any mouth. On the other hand, the wasp without antennæ behaved quite otherwise. It remained motionless, however close the pin was brought; it absolutely did not notice the honey. It was necessary to put the honey in direct contact with its mouth for it to recognise it; then it began to eat. But when the pin was removed half a millimetre from its mouth, it was incapable of following it. When a single antenna was removed the wasp perceived the honey nearly as well as before. A *Sphex* was shown capable of smelling the honey and its direction at a much greater distance than the *Pollistes*. Bees have the sense of smell so blunt that this experiment succeeds badly with them."

"2. In a glass box is placed a drop of honey which is hidden by a little hemisphere of metallic gauze with large meshes. Then some bees which have fasted a little are put into the box. The honey should be sufficiently close to the lattice, and the meshes of the latter ought to be large enough to make it very easy for the bees to pass their proboscis through this obstacle and eat at leisure. But if care is taken not to soil the lattice with honey, it makes it impossible for the bees to touch their favourite food by accident as they walk about. It is astonishing to see that all the bees promenade a hundred times at two or three millimetres from the honey, passing and repassing over the lattice, without stopping, without suspecting the presence of the liquid for which they are hungering. They would only have to pass their proboscis through the lattice in order to satisfy themselves. When the lattice is removed they recognise the honey by accident and eat it with avidity. That shows how much Wolff deceived himself. It is at the same time a confirmation of Lubbock's results. Like this author, I have assured myself that bees guide themselves almost exclusively by vision." (Their antennæ are very short, not clubbed, and have olfactory terminations only on their dorsal aspect.)

"From these experiments and from many others made by my predecessors and by myself, I conclude:—

"*a.* The so-called 'olfactory' organ of Wolff in the palate of the hive-bee is not olfactory at all, but very probably serves, as Joseph (*l.c.*) also thought, the same as other analogous organs situated in the tongue, the jaws, etc., for gustatory impressions (Meinert, *l.c.*; Forel, *Fourmis de la Suisse*, p. 117 and Figs. 9 and 10; Wolff himself, *l.c.*)."

"*b.* The mandibular gland (olfactory mucous gland of Wolff) is probably in the bee a simple gland with a stinking secretion. The secretion of this gland decomposes in the air and there becomes resinous. It is quite analogous to that of the anal glands of certain ants (*Tapinoma erraticum*, etc.) and has the same odour to us. It is probable, moreover, that it may become important in certain insects. Thus in an ant which builds its nest of a woody paste analogous to that of wasps (the *Lasius fuliginosus*) this gland is extraordinarily developed (according to Meinert, *l.c.*): it is probable that here its resinous secretion serves as cement for this paste."

"*c.* The seat of the sense of smell is in the antennæ, despite all the *a priori* considerations of Wolff (*l.c.*), of Landois,[1] of Paasch,[2] and so many others."

Schiemenz (*l.c.*, 1883), in his interesting work on the nutritive juice of bees, inspired by Leuckart, and without any knowledge either of my works or of the important research of Meinert, reaches in several respects the same result as I have done, both as to olfaction (where, like myself, he refutes Wolff) and as to the nature of the mandibular glands (his system IV. of salivary glands). He also found, as I (*Fourmis de la Suisse* and *Études myrmecologiques* in 1878, *Bull. Soc. vaud. scienc. nat.*, vol. xv. No. 80), that the function of the gizzard, which he calls *Vormagen* or *Verschlusskropp* (in the bee, therefore, as in the ant), is to shut off completely, as required, the passage between the crop and the stomach.

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[1] Landois, Archiv f. microsc. Anatomie, Bd. iv. p. 88.

[2] Paasch, Troschel's Archiv f. Naturgeschichte, 1873, Bd. i. p. 248.

Schiemenz also describes the terminal organs of the antennæ described already with nearly all the sensory organs by Hicks[1] and by me (*Fourmis de la Suisse*[2]).

I must here correct an omission which I regret. I have up to the present ignored the existence of one of Hicks' articles (May 5, 1859), having been drawn into the error by the fact that in the same volume of the transactions, but on another page, appeared another article by the same author that I believed to be the only one there. But in the article which I missed, and which I had consequently not quoted, are to be found precisely described those organs of the antennæ which I had called (*l.c.*) champagne-cork organs and bottle organs (the latter term employed later, *Ét. myrm.*, 1884, after Kraepelin), and of which I thought myself the first discoverer. Hicks had, as I now know, found the principle, although he had not seen all the details which I have described.

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[1] Hicks, Trans. Linn. Soc., June 17, 1856, June 2, 1857, May 5, 1859, May 3, 1860, and June 20, 1861.

[2] I may be allowed to quote here from Schiemenz a discovery of Fischer (*Eichstädten Bienenzeitung*, 1871, p. 130 ff., p. 230), according to which the nutritive juice of bees comes, not from the stomach as Leuckardt thought, but from the supra-maxillary glands of Meckel, glands which Fischer found always juicy and full of secretion in the young bees which nourish the larvæ, whilst they are empty and atrophic in old bees, which, as is known, no longer occupy themselves with the care of the larvæ, but go foraging out of doors. Schiemenz (*l.c.*) is of the same opinion. Now I have observed (*Fourmis de la Suisse*) that in ants it is also the young who are occupied with the work of the interior and the old who go out. The same comparative study of the supra-maxillary glands should be made in them, in the old and young, which has not been done. But these great yellow glands which cover the brain in front, and which Meinert (*l.c.*) has described so well, are so strongly developed in all species of ants that the opinion of Fischer appears to me to be the most plausible for these insects also. It can scarcely be the question in these insects of a disgorgement of the contents of the stomach, for the contents of the crop would be thereby rendered foul and opaque, which is not the case. As the ants nourish their larvæ from mouth to mouth, as they also nourish their adult companions which remain at home, one cannot examine the nature of the nutritive juice. But this juice must necessarily be of quite another nature than the ordinarily sweetened contents of the crop with which the ants feed their companions. It must certainly contain much more albumen. We know, for example, that wasps feed themselves with sweet things, whilst they feed their larvæ with flies and other insects. I believe, until further proof is forthcoming, that ants feed their larvæ, in part at least, as bees, with the secretion of their supra-maxillary glands. Nevertheless the buccal sac of the hypopharynx must not be forgotten, which, in ants, is always full of solid débris very different from the contents of the crop, analogous to the contents of the stomach, and which might well make part of the nutritive juice disgorged to the larvæ.

The following experiments have hitherto remained unpublished.

1. *On ants with antennæ removed.* On August 12th, 1886, I repeated my experiments quoted above. I removed the antennæ from a great number of *Formica sanguinea*, *Formica pratensis*, *Camponotus ligniperdus*, *Lasius niger*, and I put them all into one box together. The same facts that I have above described were exactly reproduced. It might have been called the caricature of the animals in Oberlaender's paradise, where cats, mice, foxes, lions, and hens licked each other and drank milk from the same platter. I saw a *Camponotus* which I had gorged with honey disgorge to a *F. sanguinea.* A *Lasius niger* assumed an air of dignity between the legs of a *F. pratensis* and a *C. ligniperdus.* Little by little my various ants huddled themselves happily together, some on others, despite their diversity. A few rare instances of doubt, a few feeble menaces were seen, and that almost as much between sisters of the same ant-hill as between different genera. I had first tried, as Hauser, to coat the antennæ with paraffin instead of removing them. The effect is the same, but it is less certain, and the ants are evidently more affected than by the amputation. My ants paid no attention whatsoever to the larvæ or to the pupæ. They did not even take them when I held them for a certain time under their mouths by means of a fine forceps.

Then I removed the antennæ of a great number of *Myrmica ruginodis* from the same ant-hill. These I added to the other ants. This time the effect was quite the other way. The *Myrmica* attacked, quickly biting all the ants they met, as much *Camponotus* as *Formica* and *Lasius*; they recurved their abdomens and strove with rage. Very surprised at this unlooked-for result, I was no less so to see an instant after that the *Myrmica ruginodis*, which I had just taken from their nest where they lived in sweet harmony, bite each other, tumble about and strive with one another with no less fury. I took them all out of the box and put them together in a box apart. There a regular set-to took place, strings of three to four ants biting among themselves, etc. This singular result immediately recalled the curious experiment of Belt on ants of the same tribe, which bit each other when a little corrosive sublimate was thrown on them, an experiment which I have repeated; and described (*Études myrm.* in 1884). But I only succeeded in this experiment with ants of the genus *Myrmica*. There is here a coincidence so remarkable that I believe I have found the key to the enigma of the action of the sublimate. As I have there inferred (*l.c.*), it acted on the antennæ, and one now sees it produced temporarily an analogous effect to that of amputation. It is therefore evidently a simple momentary paralysis of a part of the olfactory sensibility of the antennæ which the emanations of the corrosive sublimate produces in them, even in a small dose. I say "of a part," because they are yet able to find their way. This fact appears to me to have a real physiological interest.

One sees, further, that the pugnacious rage of the antennaless *Myrmicides* is as blind, as incapable of distinguishing friend from foe, as the idyllic peace of the *Camponotides*. Whence this strange difference? One can only conjecture. It is singular that the loss of olfaction produces in some a peaceful humour, in others a bellicose humour, when they encounter living beings which they can no longer recognise. Further, the experiment did not always succeed to the same degree, either with the sublimate or with the amputation, I cannot say why.

My *Myrmica* finished by becoming calm at the end of an hour or two, but perhaps under the influence of cold, and not without some fatalities. If any would attribute this fury of the *Myrmica* to the wound made in the nervous system and a consecutive irritation, I would reply that this is no solution of the question, seeing that the amputation of one antenna alone does not produce any analogous effect.

2. *On Flies.* July 3, 1876, at 11.30 in the morning, at Munich, I placed on my window a mole, swollen and decomposing, under a hemispherical wire gauze cover.

A. A *Sarcophaga vivipara* soon arrived, which strove to enter under the cover. But it could not find any way in. I seized it and removed both eyes with a razor. Soon it flew into my room, wheeling about, knocking against the ceiling and against the walls, and finished by falling on the floor. After this had happened two or three times I took it and removed a wing. Then I put it close to the mole, which I had uncovered. The fly became calm, went towards the mole, strove to ascend it, succeeded, plunged its proboscis into various places, and finally found a wound by which I had removed the animal's brain. There it stopped, sucked with its proboscis at two or three places, then suddenly recurved its ovipositor and, in the twinkling of an eye, laid three or four larvæ. I then immediately removed it and carefully cut off both antennæ. From that moment, despite oft-repeated trials, the fly paid no more attention to the mole than to a piece of stone or a bit of wood. Placed close to it, it no longer sought to direct itself towards the carcass. It was further unable to orient itself. It made no further attempt to lay. Placed in a box, it there finally laid two or three larvæ. Its autopsy showed me its ovaries all crammed with eggs and larvæ.

B. Shortly after came a little blue fly ♀ related to *Calliphora vomitoria.* I removed one wing. After having tasted the mole it sought to lay in various places. It found the wound, introduced its ovipositor and laid an egg. I immediately stopped it and cut off both its antennæ. From that instant it ceased to lay and paid no more attention to the mole. Briefly, although having both its eyes, it behaved exactly as the former fly.

C. A new *Sarcophaga vivipara* ♀ arrived. I removed the wings. It tasted the mole at various places for a moment, then laid a larva. I immediately cut off its antennæ. After that it ran about in every direction and worried itself about the mole no longer, in spite of all my efforts to bring it back there. I finally succeeded, nevertheless, in making it stay quietly on the back of the mole, and there at the end of a certain time it laid several eggs on the fur. But it continued to lay on my fingers.

It was a forced laying, as is often seen when the flies, kept prisoners, are compelled to lay. The act was purposeless. Then it laid no more, but was always able to find the shade (evidently by means of its eyes) which protected it from the very ardent sun.

D. A small *Sarc. vivipara* ♀ arrived at the mole. I cut off its wings. Immediately after it began to lay on the mole. I removed its antennæ, after which operation it only ran about, although I replaced it on the mole at least twenty times.

E. A *Lucilia Cæsar* ♀ came and began to eat and lay on the mole. I removed its antennæ. Then, placed on the mole, it walked about there with indifference, rubbed its feet, ate no more and entirely stopped laying, whilst hitherto its activity in both senses was truly feverish.

F. Another *Lucilia Cæsar* ♀ came and began to lay with desperate energy, without seeking to feed. I removed a wing: it layed immediately afterwards, as if nothing had happened. I unsettled it and took it several times in my fingers. Each time it only tried to regain the mole and immediately continue its interrupted laying. I removed its antennæ. Immediately its laying stopped; it did no more than brush its feet, and seemed no longer to realise that it was on a very putrid mole. It behaved like a fly which rejoiced in the sun.

G. Finally a *Sarcophaga vivipara* ♀, after I had cut off its wings, could not touch the mole without immediately laying three or four larvæ. I hastened to remove its antennæ. Immediately the laying stopped and I could no longer make the fly stay near the mole.

These experiments appear to me to prove clearly that flies smell putrid meat with their antennæ. They show, further, that the desire to lay is with them a general sensation which can be compared to a sexual appetite and which is provoked by an olfactory sensation, for it ceases immediately after the suppression of the antennæ; whilst other lesions, even the removal of the eyes, which is more considerable and more dangerous, do not hinder it. The feeble laying which took place after this was done had no longer any voluntary or passionate character; it was the simple automatic discharge of the too full oviduct.

3. *On Beetles.* A putrid hedgehog and a putrid rat served me as objects for experiment in a garden occupied by the Asylum for Idiots at Munich, June 12, 1878. A crowd of *Silpha sinuata* and *reticulata*, three *Silpha thoracica*, three *Creophilus maxillosus*, various *Philonthus*, and numerous *Aleochara* swarmed in these carcasses. I removed the antennæ of all the *Silpha* (about 35), of three *Creophilus*, and of five or six *Philonthus*. I put them all at one place in the grass. Then I moved my two bodies, putting them at 28 paces away, in a tangle of weeds.

Next day, June 13, I went to visit my bodies. Not a *Silpha*, not a *Creophilus*. Several *Philonthus* were found there, but they all had their antennæ.

June 14, hot day, slightly damp, two *Silpha reticulata* were on the rat, but their antennæ were intact. I cut them off and placed the *Silpha* at a certain distance. No insect with cut antennæ was found there. I then removed two or three feet on the same side from 7 or 8 *Aleochara* and two or three *Philonthus*, leaving them their antennæ; then I moved them to a distance.

Interrupted in my experiment, I only returned on June 22, a hot day. None of the mutilated beetles were there. Then I cut off the three feet of the same side of a dozen *Aleochara* (there were no more *Silpha*), which I moved to a distance. Then I recovered my bodies with leaves, after having moved them.

Next day I found five of my *Aleochara* with three feet cut off in the carcass of the hedgehog. I took them off and moved them again to a distance.

June 26, I visited my carcass and there again found one of the *Aleochara* with three feet.

Another time, in the month of July, I made a *Necrophorus vespillo* fast for 24 hours. Then I gave it the head of a rabbit, fairly fresh, which it attacked voraciously. Having been carried away several centimetres, it displayed uneasiness, ferreted about, searched, returned in its steps when it went away from the head of the rabbit, and soon found it. Then I cut off the clubs of both antennæ. It immediately stopped searching, no more directed itself, and appeared to be plunged in a kind of torpor. But when I put it myself on the rabbit's head it began to eat with avidity. On the other hand, when I moved it away the least bit in the world, it showed itself incapable of again finding the head.

4. On *Bombyx mori* (Silkworm). I put one or two females on the floor. The males perceived them from afar and ran straight to them, helping themselves a little by their wings, like ostriches. When the antennæ of the males were cut off they no longer knew how to find the direction of their female. But if they were placed by the side of them they paired with them with as much vehemence as those which had their antennæ. Therefore the antennæ only serve to discover, to smell the female. It is touch which evidently plays the principal rôle in the act of copulation itself among these Bombyces.

I will here point out that neither the varnishing of the eyes, nor the ablation of the antennæ, nor that of all the buccal organs (see above and in the first part of this work, which treats of vision) took away from insects the sensation of hunger nor the desire to satisfy their appetite. But it appears to me impossible to show completely that the appetite still exists when these three senses are simultaneously suppressed. We have seen, however, *Bombus* and *Pollistes* retain their appetite after the simultaneous ablation of the antennæ and of all the front of the head. It does not appear to me probable that the visual impressions which alone remained, and allowed them to seek and find their flowers, could be the cause of the sensation of hunger. It is, therefore, as with ourselves, produced by the reflex action of the digestive organs at the time of inanition.

The experiments which I have just recorded, and which I made eight to ten years ago, noting in proportion all their details, such as I have just transcribed, confirm fully, as will be seen, those of Lefebvre, of Perris, etc. Gustave Hauser (*l.c.*, 1880) has made analogous experiments and has arrived at the same result. Only, as he shut up his *Silpha*, cockchafers, and butterflies in a box, accident might have made them meet more than once the coveted object (cadaver or female), even when their antennæ had been cut off. Hauser has no more knowledge than Schiemenz of my already published experiments, nor of the antennary organs which I have described; and that part of the works of Hicks which had escaped me is also unknown to him. His description of the nerve terminations of the antennæ is in great part erroneous and has been corrected by Kraepelin (*l.c.*) and by me (*Ét. myrm.*, 1884).

In all that concerns the anatomical details of the antennary organs, I refer especially to the work of Kraepelin (*l.c.*) and to my own (*Ét. myrm.*, 1884), as also to those of Hauser and Schiemenz (*l.c.*) But I add that the discovery of these organs rests with Erichson (*l.c.*) and with Leydig.[1]

Nevertheless, I may say in a few words that I have divided these organs into five categories, of which two are invaginated in the interior of the antenna, one lying down or flattened, and two protuberant in the form of slightly modified and sensory hairs. I believe I have shown that all the five categories are simply derived from more or less modified hairs. Often the terminations of the antennary nerve are limited to a swollen or perfoliated portion of the antenna. Then this part alone is the organ of smell. Such, for example, are the lamellæ of the Lamellicorns, the ramifications of the pectinated antennæ of the *Bombyces*, the swollen joint of the antenna of the Diptera, the club of the antennæ of most of the Coleoptera and Hymenoptera. In general the joint or joints at the base of the antenna are destitute of olfactory organs. Often the first joint is long and the antenna is bent between it and the others. Then this basal joint is called the "scape," and the remainder the "funicule." In ants, where this condition is general, the scape is absolutely destitute of olfactory organs, and these organs are very scattered at the base even of the funicule, whilst its extremity is quite sieve-like. Further, the ablation of the funicule is quite sufficient to deprive the ants of their sense of smell and the faculty of recognising each other. In the aphides the olfactory terminations are limited to the internal dorsal surface of the funicule. Thus what we have said does not always apply to the entire antenna, but only to its olfactory portion. The so-called filiform antennæ (ichneumons, locusts, *Noctuæ*, *Longicornes*) have on the contrary the olfactory organs distributed over almost their whole length.

I have been led, as Schiemenz, to consider the category of intermediate organs, those *sensory hairs lying in a longitudinal groove* (sometimes scarcely marked) *and often transformed into prickles or plaques* as being probably the fundamental olfactory organ. They are, indeed, distributed (although more or less modified) in all insects, and are more abundant as the sense of smell is evidently more developed. They are more abundant in males than in females, as Schiemenz has very well pointed out. They are developed almost alone, but of immoderate length, in the ichneumons, which must have an exquisite sense of smell. It is the same with the leaflets of the antennæ of bombycides, especially of males, etc. The two other categories of sensory hairs, the cones or "olfactory clubs" of Leydig and the narrow or pointed sensory hairs, appear to me rather, especially the last, to serve for touch (perhaps the cones serve a little for a kind of taste, for they are found, it appears to me, especially in insects which use their antennæ much for tasting the chemical quality of objects which they seek, as especially in the social hymenoptera). On the other hand, the curious internal or invaginated organs (champagne-cork organs and flask-shaped organs) are still a physiological enigma. Their very unequal distribution, the fact that they are hardly ever found except in ants and aphides, that they are very abundant in the domestic bee, few in the humble-bee, absent in wasps, proves to me that they have nothing to do with olfaction. Their communication with the antennary nerve has not yet been demonstrated. Kraepelin goes so far as to suggest they are glands. Lubbock,[1] on the contrary, makes them auditory organs—microscopic stethoscopes!

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[1] Leydig, *Ueber Geruchs- und Gehörogane der Krebse und Insecten.* Müllers Archiv, 1860, p. 265.

In conclusion, what form should our ideas take on the sense of smell in insects? I think we ought especially to note several general facts.

1. In many insects which guide themselves essentially by vision, as with dragon-flies and cicadas, the antennæ are rudimentary, and the sense of smell also. By night these insects are motionless. By day all their acts are guided by vision (some *perhaps* by hearing, as in crickets).

2. The sense of smell, in spite of the protestations and ex-

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[1] Lubbock, *On some points in the Anatomy of Ants.* The Monthly Microscopical Journal, Sept. 1, 1877, and also *l.c.*

periments of Graber, resides in the antennæ, especially in their swollen or perfoliate parts where the antennary nerve ramifies.

3. In certain insects, as in most of the diptera, the antennæ are stiff and probably serve entirely or almost entirely for olfaction properly speaking.

4. But in other insects they are mobile and serve them at once to *smell at a distance* and *taste what they can touch*. This is the case with the hymenoptera to a very high degree. But we have seen that by the aid of its antennæ the male bombycide smells the female at great distances, flies and various beetles putrid meat; that with their help *Pimpla*, *Leucopsis*, the parasites of *Cynips* and, as has been so well shown by Fabre in his *Souvenirs entomologiques*, the anthrax and many other parasitic insects discover through dry wood, juicy vegetable, or even through a thick layer of mortar, a victim very deeply hidden, but nevertheless destined to become the prey of their progeny. These "horns," these "ears," form, therefore, a famous nose, in spite of Wolff and Graber.

Let us admit—it is, perhaps, very bold—that the olfactory bulb and nasal mucous membrane of vertebrates are derived from the invagination of the antenna and the antennary ganglion of an invertebrate.[1] The nerve terminations, formerly portruding, are sunk in a cavity which they line, and which is placed in communication with the pulmonary organ of respiration, which allows of a current of air continually renewed to bring odours to them. For my part, I believe that this homology is true. Then the antennary ganglion will become the olfactory bulb, its nerve terminations will be the numerous little olfactory nerves, the antennary nerve will become the *tractus olfactorius*, and the antennary cerebral lobe will become the olfactory lobe. Gudden has shown that the peripheral part of the olfactory bulb of vertebrates, the glomeruli, grows from the peripheral nerves to the brain and becomes secondarily applied to the olfactory lobe of the hemisphere.

[1] After having ended the present work, I found that Bellonci (Atti dei Lincei Cl. sc. fis. ecc. Ser. 3a, vol. xiii. p. 555) has treated this subject by studying comparatively the olfactory lobe of the lower vertebrates and the antennary lobe of insects. He finds that the histological structure of these organs in the arthropoda has very great relation to that of the olfactory lobe of vertebrates, and concludes therefrom a physiological, if not morphological, homology.

An instant's reflection will demonstrate to us that if, at the outset, the antennary organ of olfaction possessed specialised energies from direct contact with objects, it must lose them as a result of its invagination, as has probably already happened in flies and dragon-flies on account of the rigidity of their antennæ. This explains, it appears to me, why we do not smell when the nasal mucous membrane is touched. It would be of no use.

On the other hand, I believe that, without any doubt, in the hymenoptera the sense of smell takes place not only at a distance, but by the direct contact of the object already perceived at a distance. In reality the method by which the ants, for example, recognise each other by the contact of their antennæ, distinguish a crowd of objects one from another only after having thus tasted them, shows something more than simple touch; in a word, a sort of smell which is perfected by direct contact. It is, further, certain that true tactile impressions, arising from a variety of terminal antennary organs, also assist the sense of smell.

To obtain a just idea of the importance of antennæ among most apterous insects, the student should read the admirable pages of Huber[1] on the antennal language of ants, and the experiments of Lubbock (*l.c.*) on the power of communication of ants and on the manner in which they find their way.[2] Then they may be compared with my experiments on ants with cut antennæ quoted above.

Let us carefully reflect what is implied, to a social being such as an ant, by the total loss of power to recognise its companions, to distinguish its enemies, to recognise the little ones of the community (the larvæ and pupæ), to find its way at 2 mm. distance. Only taste, appetite, general sensibility, remain to it, which give it scarcely any knowledge; and an indistinct vision which allows it to take fright when anything moves before it, without leaving it the means of knowing how to escape. Also, when anything moves in front of it, it only makes a sudden start and a menacing or rather defensive opening of the mandibles. The poor ant without antennæ is therefore as lost as a blind man who is also deaf and dumb. This appears from its complete social inactivity, its isolation, its incapacity to guide itself and to find its food. It can therefore be boldly supposed that the antennæ and their olfaction, as much on contact as at a distance, constitute the *social sense* of ants, the sense which allows them to recognise one another, to tend their larvæ and mutually help one another, and also the sense which awakens their greedy appetites, their violent hatred for every being foreign to the colony, the sense which principally guides them (a little helped by vision, especially in certain species) in the long and patient travels which they have to undertake, which makes them find their way back, find their plant-lice and all their other means of subsistence.

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[1] P. Huber, *Recherches sur les mœurs des fourmis indigènes.* Geneva, 1810.

[2] The beautiful experiments of Lubbock (*l.c.*), which I suppose known, and to which I refer, have led him, as regards the development of the sense in ants, exactly to the same conclusions as those which I formulated long before in my *Fourmis de la Suisse*, pp. 118-121. He finds, like me, that ants guide themselves principally by the sense of smell, and that they see badly.

As the philosopher Herbert Spencer has well pointed out, the visceral sensations of man, and those internal senses which, like smell, can only make an impression of one kind as regards space (two simultaneous odours can only be appreciated by us as a mixture) are precisely those by which we can gain little or no information relative to space. Our vision, on the contrary, which localises the rays from various distant points of space on various distinct points of our retina at the same time, is our most relational sense, that which gives us the most vast ideas of space.

But the antennæ of insects are an olfactory organ turned inside out, prominent in space, and further, very mobile. This certainly allows us to suppose that the sense of smell may be much more relational than ours, that the sensations thence derived give them ideas of space and of direction which may be qualitatively different from ours.[1]

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[1] It is scarcely worth insisting on this point. In reality a sense of smell which admits of distinguishing space is a kind of sixth sense very difficult for us to describe. But all evidence points to the fact that insects with mobile antennæ have such a sense. In this way the sense of smell directs them much better than the mere perception of odours. This fact also explains how ants distinguish the right side and the left side, the front and the back, by their sense of smell, and know, when following a track or trace, in what direction they are following it. Finally, pursuant to the laws of association, it allows in insects an olfactive memory of places such as relational sense alone possesses (1900).

I have not the right to deny with absolute certainty the possibility of something analogous to the sense of smell in the palpi, especially in certain insects which have long palpi and short antennæ, in the *araneida*, etc. Nevertheless, my experiments have made me see that sensation apparently seated in the palpi is rather seated in the buccal organs of taste, of which we have to speak. The nerves of the palpi do not come from the brain, but from the subœsophageal ganglion. I am inclined, like Plateau, to see in the nerve terminations of the palpi simple tactile organs. The whole organisation and habits of spiders show them chiefly dependent on their extremely delicate tactile impressions, aided only a little by their bad sight.

Now let us return to Graber. In the *Biologisches Centralblatt*, Bd. v. No. 13, Sept. 1, 1885, he speaks in the following words of his experiments on the sense of smell: "*es ist nicht zu viel behauptet, wenn ich sage, das neben den von mir eruirten Thatsachenreihen die landläufigen Anschauungen, Vorurtheile und Meinungen, mögen sie auch noch so tief eingewurzelt sein, nicht länger mehr bestehen können.*"[1] What does Graber mean? He certainly does not wish to talk of the popular opinion on the sense of smell in insects, for such opinion does not exist. Consequently these scornful words can only be addressed to the works of his predecessors on these subjects. Has Graber really the right to speak in these terms of experiments as well done and of opinions as judicious as those of Perris, of Kraepelin, of Lubbock, of Hauser? His experiments have number on their side, it is true. But we have the right to say that they testify to a very superficial knowledge of the habits of insects, often lack control, and especially judgment, that they are very little varied, that the means and the reagents employed are often very clumsy, and take no account at all of the habits and the wants of each species. We have the right to bring home to Graber his contradictions. He first sought and believed he had found, with Wolff, the sense of smell in the palate. Now he wishes to find it everywhere, and nevertheless he must acknowledge "that there are insects in which the antennæ play a preponderating rôle in distinguishing the weaker odours, food, etc." In my opinion, the clumsy sense of smell which Graber believed to have found in the cerci of orthoptera, the stigmata, etc. etc., is only another instance of one of the varieties of the general tactile sensation due to strong chemical actions on delicate nerve terminals. It is as much a *sense of smell* as the sensation of the conjunctiva of our eye affected by chloroform, ammonia, or sulphurous acid. Compare my experiment above with *Lucilia Cæsar* with that of Graber on the same fly, and I think there will be no difficulty in coming to my opinion. But Graber still more contradicts himself apropos of hearing. We shall refer to that again. By these words, however, I do not at all pretend to lessen the important results of Graber on photodermatic sensations, but to contest with him the right to sweep away in passing, as he has done, the observations of all his predecessors, many of which are better than his own.

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[1] It is not saying too much if I maintain that the current views, prejudices, and opinions, be they ever so deeply rooted, cannot possibly exist any longer beside the series of facts which have been ascertained by me.

Plateau has, however, quite lately reprinted in the *Bulletin de la Société de Belgique* (June 5, 1876) the experiment of Graber on *Periplaneta* by a counter-experiment analogous to that which I have made on bees. He placed their bait in the middle of the receiver within a ring of cardboard of which the edges were sufficiently raised to hide the bait, to prevent it from being found by accident; in short, to dissuade the *Periplaneta* from climbing except with a particular object. The *Periplaneta* with antennæ were able to find the bait. None of those with antennæ cut off could discover it, except in one fortuitous case, at the moment of the beginning of the experiment.

Taste

This sense has hitherto received relatively less attention than the others. We ourselves are often hardly able to distinguish a taste from an odour. Also we must not demand too much of the study of taste in insects, especially when we establish a sense of smell by contact in the antennæ. Nevertheless it is evident that many insects need a sense which permits them to distinguish the chemical quality of their food before swallowing it, for these aliments might contain some corrosive or poisonous substance which is not volatile and cannot be perceived beforehand by the sense of smell. *Taste is with us only a chemical sense of contact serving to discern the chemical quality of non-volatile substances, to distinguish them one from another by the help of a specialised energy related by its quality to that of smell.* Here are, partly according to Will, the works which have appeared on taste in insects: Leydig,[1] Meinert,[2] Aug. Forel,[3] O. J. B. Wolff,[4] G. Joseph,[5] Künkel and Gazagnaire,[6] Breitenbach,[7] Huxley,[8] Becher,[9] K. Kraepelin,[10] Haller,[11] Kirbach,[12] Béla Haller,[13] Will,[14] J. Gazagnaire,[15] F. Plateau[16]; we can add here the opinion of several authors, Knoch,[17] Lesser,[18]

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[1] Leydig, *Zur Anatomie der Insecten.* Reichert's Archiv f. Anat. und Physiol., 1859, H. 1, pp. 62-65 and pl. vi.

[2] Meinert (*l.c.*), *Bidrag, etc.*, 1860, pp. 6 and 66.

[3] Aug. Forel, *Les Fourmis de la Suisse*, 1874, pp. 117, 121, 377, 446. *Ibid.*, Zeitschrift f. Wiss. Zoolog., Bd. xxx. Suppl. p. 60, 1878. *Ibid.*, *Étud. myrm.* in 1884, p. 19.

[4] O. J. B. Wolff, *Das Riechorgan der Biene* (*l.c.*), pp. 92 and 176.

[5] G. Joseph, *Zur Morphol. des Geschmacksorgans bei den Insecten.* Amtl. Bericht der 50. deutsch. Naturf. Versammlung, Munich, 1877, p. 227.

[6] Künkel and Gazagnaire, *Du siège de la gustation chez les insectes diptères.* Comptes rendus des Sc. nat., Bd. xcv., 1881, p. 347.

[7] Breitenbach, *Beitr. z. Kenntn. d. Baues d. Schmetterling-Russels.* Jenaische Zeitschrift, Bd. xv. p. 154.

[8] Huxley, *The Crayfish.*

[9] Becher, *Zur Kenntniss der Mundtheile der Dipteren.* Denkschr. der Acad. d. Wiss. Wien, Bd. xlv., 1882, p. 123.

[10] K. Kraepelin, *Ueber die Mundwerkzeuge der saugenden Insecten.* Zool. Anzeiger, 1882, No. 125, p. 575. *Ibid.*, Z. Kenntn. der Anat. u. Physiol. des Russels v. Musca, Ztschr. f. Wiss. Zool., Bd. xxxix., 1883, p. 713.

[11] G. Haller, *Z. Kenntn. d. Sinnesborsten der Hydrachniden.* Wiegmanns Arch. f. Naturgesch., 1882, H. 1, p. 43.

[12] Kirbach, *Mundwerkzeuge der Schmetterlinge.* Zool. Anz., 1883, N. 151, p. 556.

[13] Béla Haller, *Untersuch. üb. marine Rhipidoglossen.* Morphol. Jahrb., Bd. ix., 1884, p. 76.

[14] F. Will, *Das Geschmacksorgan der Insecten.* Zeitschr. f. Wiss. Zool., xlii., 1885.

[15] J. Gazagnaire, *Orig. de la gustation chez les coléoptères.* Proc. verb. de la Soc. zool. de France, March 11, 1886. *Ibid.*, *Du siège de la gust. chez les coléoptères.* Comptes rendus de l'Acad. d. Sciences, March 15, 1886.

[16] F. Plateau, *Palpes des insectes broyeurs.* Bull. de la Soc. Zool. de France, t. x., 1885.

[17] Knoch, in Lehmann (*l.c.*), *De sensibus externis, etc.*, 1798.

[18] Lesser, *Théologie des insectes*, ii. p. 8, 1742.

Léon Dufour,[1] Packard,[2] Treviranus,[3] according to Plateau (*l.c.*).

Leydig and Meinert[4] first gave good descriptions of the organs which I consider those of taste and which are situated on the jaws and at the base of the tongue. Meinert has already expressed his opinion that they are organs of taste. In my *Fourmis de la Suisse* I have further pointed out a row of these organs at the end of the tongue, and I have regarded them, equally with the previous ones, as organs of taste. Then I have shown experimentally the existence of taste in ants. Joseph and I (*Zeitschr. f. Wiss. Zool.*) have considered the organ of Wolff in the palate of certain insects as being also an organ of taste.

When morphine or strychnine are mixed with honey, ants do not at first perceive it with their antennæ. The smell of the honey attracts them and they begin to eat. But when they taste it they immediately leave it. The preference of ants for certain foods is easily observed; they eat of one in default of the other, but abandon all, even often their duties and the defence of the nest, for honey, of which they are extremely fond. I have seen ants, attacked in their nest and dangerously pressed by others, stop an instant, despite the danger, opposite to some honey which I offered them and snatch a mouthful (Forel, *Les Fourmis de la Suisse*, pp. 117, 121, 377, 446).

Ants do not know how to distinguish the smell nor the savour of all that is hurtful to them. Some workers of *F. pratensis* gorged themselves with honey and phosphorus which I gave them. After that they remained for some time motionless, mandibles wide, mouth open, paying no attention to their surroundings. Those that had eaten most perished, the others recovered little by little. We can draw conclusions, however, how much the toxic action of chemical bodies on these insects differs from that on ourselves, if one but takes account of the following facts which I have observed repeatedly. Whilst arsenious acid kills the flies which eat it, hundreds of *Myrmica scabrinodis* crammed themselves with honey full of this substance without a single one among them appearing to suffer. Strychnine introduced in strong doses into small wounds produced no cramp, and the ants only died therefrom very slowly. Small doses of morphine introduced even into a wound of the abdomen sufficed on the other hand very quickly to produce the most violent convulsions and the most curious preliminaries to a tetanic condition.

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[1] Leon Dufour, *Recherch. anat. sur les carabiques et sur plus autres coléop.* Ann. des Sc. nat., viii., 1826.

[2] Packard, *First Ann. Rep. of the U.S. Entom. Commiss.* for 1877, p. 272, 1878.

[3] Treviranus, *Verm. Schriften Anat. u. Physiol.*, Inhaltes ii. p. 150, 1817.

[4] Braxton Hicks (*l.c.*) has also described in words and drawn the organs at the base of the tongue of a Megachile the same year as Meinert (1860), but without giving any detail as to their structure.

Everyone has seen how caterpillars especially recognise the plant which suits them by taste. When they are hungry, they try various leaves, but abandon each quickly until they have found one, or more, which suits them. We should never finish if we tried to follow insects through all their gustatory preferences, be they for flower, leaves, game, wood, grain, roots, excrement, or putrid flesh. Brillat-Savarin could have written volumes thereon. Where, then, is the seat of taste?

Perris (*l.c.*) says that the amputation of the palpi often allowed him to bring close to the mouth a forceps moistened with odorous substances without the insect being affected. "But several times it showed a little sensitiveness, because it is very difficult radically to remove these organs." Perris believed in a sense of smell at short distance in the palpi. I have already shown that this kind of experiment is little convincing. Plateau found that in fifty individuals of different species of coleoptera and orthoptera the amputation of the four palpi had not any sensible result. The insects had their sense of smell remaining as before. They ate as well and distinguished their foods one from another as clearly as before. Will (*l.c.*) obtained, in his work appearing at the same time as Plateau, the same result. I can entirely confirm these experiments as regards wasps and ants. The amputation of the palpi in no way modifies their olfactory, gustatory, or masticatory faculties.

I have even supplemented the experiments of Plateau and Will on an important point. It may be objected to these authors that insects deprived of their palpi recognise their food by the smell perceived by the antennæ. And this is a very serious objection.

I therefore amputated both antennæ and the four palpi in several wasps. Then I gave them honey mixed with quinine. It was naturally necessary to bring them so that their mouth touched the honey, for they were not in a condition to find it alone. They then tasted it, but abandoned it each time immediately after. On the contrary, when I put pure honey without quinine or morphine, they ate it greedily. This shows that the gustatory faculty is independent of the antennæ and the palpi, and that it resides in the mouth.

Plateau found that the palpi do not act at all in mastication. I have already demonstrated (*Fourmis de la Suisse*, p. 108) that ants eat almost exclusively with the tongue, *i.e.* lap, as Lespès has already seen and as MacCook has confirmed. Their feeble jaws, short and without teeth, cannot triturate. The mandibles are inactive whilst they eat. Therefore they can only lick up liquid or viscid substances. In the grinding insects (coleoptera, orthoptera, caterpillars), the mandibles and jaws serve to grind, to chew solid substances which are afterwards swallowed. The mandibles of ants only serve to carry, to bite, to tear, to saw, and shape, never to chew. But in all insects known to me the palpi only hang inactive below the mouth during feeding, as Plateau said. This, joined to what we have seen as to the sense of smell, brings me to consider the palpi, with the tarsi, the anal appendages of certain insects, etc., as especially tactile organs.

As Will insisted, it is scarcely possible to remove the tongue and epipharynx without the insect losing the power of eating. I therefore do not see how the *crucial experiment* can be made to demonstrate the sense of taste. One can only proceed by elimination, as Plateau did, and as I have done in a little more complete manner with wasps.

I consider therefore as organs of taste :—

1. The nerve terminations of the proboscis of flies described by Leydig (*l.c.*) and which are the homologues of the following.

2. The nerve terminations of the jaws and at the base of the tongue described by Meinert (*l.c.*) in ants.

3. The nerve terminations of the extremity of the tongue described by me (*Fourmis de la Suisse*) in ants.

4. The terminal nerve organ of the palate or epipharynx described by Wolff. The last appears to me, in certain insects at least, to play a preponderating part, and it is not for nothing that it is so developed in bees which imbibe the honey in so many flowers.

F. Will (*l.c.*) has written a monograph on the subject which occupies us. He has made a series of very careful and ingenious experiments to demonstrate the sense of taste in insects. He has employed indifferent substances as a control. After having habituated wasps to come and eat honey on a basket, he replaced it by alum. The wasps came there, were deceived by habit, tasted the alum, but turned away very quickly, making contortions. Then he deceived bees and humble-bees by putting honey into flowers, then adding quinine, salt, etc., to it afterwards. Each time the insects began by tasting it, and left the flower when they had perceived the bitter taste.

Will found that the gustatory perception remains a rather long time. Insects clean their mouths for several minutes. When they are afterwards given pure honey, they taste it several times before definitely beginning to eat. All hymenoptera have a horror of quinine. Most insects fly from tobacco. Nevertheless certain brenthides live on cinchona and certain annobium in tobacco. Will found that, as a whole, the larvæ are more difficult to please in the choice of their foods than the perfect insects.

Will enunciates the general and new opinion that "*in most insects the limits of distinct perception are very narrow, but that between these limits the distinctive faculty is extraordinarily delicate.*" This present opinion is of interest, but I believe it to be premature. The first part of the proposition is in any case the only one which appears to me probably true, and yet may be inexact if the experiments of Graber quoted above have the value which their author attributes to them.

Will believes he has found, as did Hauser in the case of the terminal organs of the antennæ (the researches of both authors have been made at Erlangen in Selenka's laboratory), that the chitin of the gustatory hairs which surmount the canal pore of the nerve terminal organ is pierced by either a hole, or by a canaliculus, and that the axis-cylinder is free on the surface. I consider this opinion, as also for the organs of the antennæ, to be an error. The chitin is, truly, very thin and flexible, as much at the extremity of the so-called olfactory clubs of Leydig, as in the middle of the sensory plaques (olfactive) of the antennæ of aphides, and as at the extremity or on one side of the gustatory hairs of hymenoptera. Endosmosis through this fine membrane suffices as well to explain the sensation as to explain the secretion across the terminal chitin of the excretory canal of gland cells (*cf.* Leydig, *l.c.*, and Forel, *Zeitschrift f. Wiss. Zool.*, Bd. xxx.).

Will, following the above opinion, believes he can affirm that the organs of the jaws as well as those at the base and at the extremity of the tongue are the only gustatory organs. He peremptorily refuses this quality to the organ of Wolff, without "having other reason to give than that the supposed opening in the other organs is absent here." Gazagnaire, on the contrary (*l.c.*), considers in beetles the anterior region of the dorsal pharyngeal wall (therefore the organ of Wolff) as the only organ of taste in these insects. He finds a group of unicellular glands, of which the excretory canals open about each nerve termination to lubricate it.

I believe for my part that all these organs are gustatory. To begin with, they bear a remarkable resemblance to each other. Further, I do not see what qualification another sense in the interior of the mouth could have apart from touch, which seems already represented by scattered tactile hairs, and which itself could scarcely have any reason to be in the palate of a bee with its proboscis and liquid foods.

CHAPTER VI

HEARING—TOUCH AND ITS DERIVATIVES

Hearing

MUCH has been written on the hearing of insects. Sulzer, Scarpa, Schneider, Bonsdorff (*l.c.*), Carus, Strauss-Dürckheim, Oken, Burmeister, Kirby and Spence, Newport, Léon Dufour, Hicks (*l.c.*), Lespès, Goureau, Lacordaire, Paasch, Landois, Wolff (*l.c.*), and Graber have considered the antennæ as the organs of hearing, as the "ears" of insects. What a crowd of distinguished names to uphold an opinion so absolutely at variance with the truth! But if we look more at their opinion we see that it is based, not on experiments, but rather on certain theoretical considerations: the want of "damp mucous membrane" on the antennæ, the small more or less flat membranes of certain terminal organs of the antennæ (*tympanules* of Lespès), etc. Several superficial and badly understood experiments, where mechanical vibrations are regularly taken for sounds (Newport, Paasch, Landois, *l.c.*[1]), appear to give support to the theory and are quoted and requoted everywhere. Finally it is noteworthy that none of these authors have been entomologists, hunters, and biologists, practical naturalists thoroughly acquainted with the habits of insects.

I will be very brief, for all that I can say on the subject is absolutely negative, since only crickets and several other orthoptera appear to perceive sounds. P. Huber (*l.c.*), Perris (*l.c.*), Dugès (*l.c.*), Lubbock (*l.c.*), and I have tried the production of all the sounds imaginable. The other insects have always appeared to remain deaf, when we have avoided mechanical vibrations, to which insects are extremely sensitive. Lubbock has even tried to produce sounds too high to be perceived by us. He has succeeded therein, but no insect has reacted to them, and he has been obliged to end by agreeing with the opinion of Huber, of Perris, and of myself, that hearing cannot be demonstrated in bees, wasps, and ants. In spite of this he persists in believing that insects hear sounds which we do not. I have scraped the highest string of a violin even at 3-4 cm. from bees engaged in pillaging flowers; I have cried out and whistled my loudest at several cm. from various insects, whilst protecting them from my breath. As long as they did not see me, they paid no attention whatever. What is to be said of Léon Dufour, who thought he demonstrated hearing in crickets and in *Anobium* because the former ceased their note when, standing 2 or 3 metres away, he struck the ground at his feet, and because the latter were silent when a chair was moved. He has forgotten that deaf-mutes feel the rolling of a carriage at a distance.

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[1] And *Thierstimmen*, 1874, Frieburg i. Br. In this work Landois thinks he shows that ants hear because they leave their nest in fright when a large cross spider is thrown thereon. Truly it requires very little reflection to suppose similar things. A deaf-mute, even blind, would skip out immediately if an ox were thrown on his house.

Hearing is a physical sense. Sonorous waves, especially those of low sounds, are nearer to large mechanical vibrations than luminous, caloric, or electric waves. Hearing, therefore, must be in its origin connected with touch, but we make a distinct difference between the perception of a very low sound by touch and its perception by hearing. We must not forget that the specialisation of the organ of hearing has reached in man a delicacy of detail which is evidently not found again in lower vertebrates. It is, I believe, the sense which removes us most from the lower animals. In animals as high as fish the auditory nerve is confused with other nerves, and the portion of the labyrinth most specially affected by our audition, the cochlea, has disappeared.[1]

Graber, in his beautiful work on the tympaniform organs of the orthoptera,[2] after having carefully described these organs, extirpated them, cut especially the anterior feet of crickets and locusts and found that they heard as well, if not better, the strings of a violin and the cry of other crickets after the operation as before. Graber removed the antennæ of his crickets. They heard, *i.e.* reacted by a sudden start, after as before. He cut of their head. The latter alone reacted by the antennæ to sounds. The body no longer reacted, save to mechanical vibrations. Logic must conclude that the organ of hearing is somewhere in the head. But Graber insists in spite of that in searching in the antennæ, and in a subsequent work[1] he thought he had discovered in an organ in the antenna of flies, long ago described by Hicks (*l.c.*) and Leydig, an otolith, calls this organ "otocyst," and declares it to be an organ of hearing. Paul Mayer[2] refutes this. But Graber has not lost courage. To him it is a settled thing that insects hear. In his latest works[3] he claims to have found that the decapitated body of *Periplaneta* reacts to sounds, and now concludes that a special organ of hearing does not exist in these insects, but that in them hearing is disseminated over the whole body. No one could change his opinion more than Graber. What does he make of his old experiments? Or did he really believe that crickets hear with the head, cockroaches with the whole body, and flies with the antennæ, without mentioning the tympaniform organs of the front feet of crickets and of the abdomen of grasshoppers. It is the case of crying out: What a lot of ears for a deaf man!

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[1] Rather, has not yet appeared.—TRANS.

[2] Graber, *Die tympanalen Sinnesapp.*, etc. Denkschriften der K. B. Acad. d. Wies. in Wien, Bd. xxxvi.

Will (*l.c.*, p. 9) quotes in passing an experiment that he made on *Cerambyx scopoli.* He shut a ♀ in a box, and claims that each time he irritated it with a pin stuck in the wall, so as to make it stridulate, the male which was placed at 15 cm. from the box heard it, became excited and went to the box. He believes that insects only hear the stridulation of their species. I must oppose to this experiment that of Perris (*l.c.*), who has "made flies buzz, longicornes scrape the corselet, etc., at some distance from individuals of the same species and of different sexes and established nothing in particular."

To sum up. What may be considered as proof of hearing appears to me (as to Dugés) to rest, with few exceptions, almost certainly on mechanical vibrations of the air or ground. These are simply perceived as such by the tactile organs of insects. This almost corresponds to the last opinion of Graber on "hearing" in *Periplaneta*. But it is not right to call such sensations hearing. Therefore let us leave the question open until it may be solved by serious and decisive experiments.

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[1] Graber, *Ueber neue otocystenartige Sinnesorgane der Insecten.* Arch. f. micr. Anat., 1878, Bd. xvi. p. 36.

[2] Paolo Mayer, *Sopra certi organi, etc.* Reale Accademia dei Lincei, Anno cclxxvi., 1878-79.

[3] Graber, Archiv f. microscop. Anatomie, Bd. xx. und xxi.

Touch and its Derivatives

All authors agree in recognising that insects perceive tactile stimuli with great delicacy. Nevertheless, this is not the case with all nor everywhere. Certain beetles which have an enormous chitinous carapace appear less sensitive to light touches than those which have thin skin. Among insects endowed everywhere with a very delicate sense of touch, we may quote caterpillars. But further, the sense of touch is generally distributed irregularly on the surface of the body. Certain parts, as the elytra and wings, appear in great part insensitive.[1] Thus, I have succeeded in cutting the wings, about the middle, of wasps while they ate honey without seeing me, and they perceived nothing. The most delicate sense of touch appears to reside in the antennæ, conjointly with the sense of smell. Then come the palpi, the trochanters, and the tarsi, which are covered with nerve terminations and are very sensitive to touch. But this is also the case with the abdomen, the anal appendages, when they are present, and all the soft parts of the body. Nevertheless the sensitive parts also have often a thick chitin.

As Leydig and Hicks have shown, the tactile sensibility takes place by means of sensorial hairs which are placed on a large canal pore of the chitin which borders on a nerve termination.

But the general sensitivity of insects is characterised by peculiarities other than by this sense of touch analogous to our own. We must before all consider that insects are beings very small in size, and, besides, thanks to their tracheal circulation (I mean that of the air), very light. On the other hand, the surface of their bodies is generally rigid and hard. *From this rigidity it follows that a touch or a breath does not act by compressing a localised portion of the skin (its tactile hairs) and its nerves, as is the case with vertebrates and molluscs, but rather displaces by the shock to the entire insect.* But seeing the extreme lightness of most insects, it is sufficient for a mere nothing, for the lightest movement of the air, for the most insignificant mechanical vibration to produce a like effect and to change their state of equilibrium. It is true, moreover, that this shaking movement also affects the nerve terminations, especially those of the tarsi, by the friction. We must necessarily conclude that this kind of sensations, and particularly the muscular sensation, *i.e.* that of the muscular tensions destined to re-establish equilibrium, should play an immense part in insects. And it is easy to show that this is the case. Every entomologist will, as an expert, bear me out when I say that the lightest breath, the smallest shaking, makes insects fly immediately or makes them fall from their branches or their leaves; while the loudest cries and the sight of a man, so long as he moves gently, leaves them generally indifferent (I do not speak of insects with good sight). But still more: it may often be observed that, in a fairly strong wind, beetles which are on a shrub do not fall, whilst they fall when we lightly shake them. It is because the beetles have immediately discerned between the two forms of shaking. The one is innocent, the other reveals a living and large being. Perceiving the latter they fold their feet and allow themselves to fall. If anyone wishes to study all the knowledge that this kind of touch can give to a small animal, let him carefully observe the habits of spiders.

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[1] Hicks (*l.c.*) has nevertheless found terminal nerve organs in the nervures of the elytra and wings.

I believe it is wrong to attribute to spiders a delicate sense of hearing. Here, again, hearing has been confounded with the sensation of mechanical vibrations. It is necessary to take care when one watches them, as when one watches insects in general, to protect them also against the breath of the watcher by placing the hand or other screen before the nose or mouth. If, further, the vibrations of air or walls be avoided with the greatest care by softly opening doors and walking circumspectly, it will be seen that an infernal concert can be made in a room full of spiders, without these animals giving the least sign of attention. But it is necessary to keep motionless so that we may not attract their attention by large movements, and not to disturb the air by moving about the musical instrument too much. I have never for my part been able to note the musical sense which has been attributed to spiders.

One may amuse oneself, on the other hand, feeding spiders by throwing various insects into their webs. They may be watched when they are spinning their webs or when they pass from one tree to another through the air by first suspending themselves by a thread (they let themselves fall spinning), then throwing from their other silk glands a curl of thread which the breeze gently wafts into space, whilst they continue to spin. This line may reach to several metres, despite its extreme delicacy. The spider remains motionless, the feet stretched out, suspended in the air by a thread and spinning its line sideways. Suddenly, without our seeing anything, it pulls itself together, catches the base of its line with its feet, and starts gathering it rapidly in by their alternating movement. It has felt that the end of this line has touched something at several metres' distance.

This something is the branch of another tree, to which the line has adhered. While the spider rolls up the base of the line with its feet, the line becoming shortened, little by little, holds fast, becoming a thread fixed to a branch of the other tree, and in a short time our acrobat has thus passed from one tree to the other high in the air.

If we throw insects in great variety into the webs of spiders, we shall soon see that by their shock, by the more or less strong tension of the threads, the spider distinguishes without seeing them if they are large or small, heavy or light, and that it perceives all their movements. It has indeed always seemed to me that it distinguishes hymenoptera from diptera, for whilst it is very circumspect with the former, it throws itself on the latter without the least reserve nor the least prudence. But for the same size, hymenoptera are more heavy than diptera, and their movements, both of wings and body, are quite different.

When the spider feels the least unexpected shock to its web it starts. Some (the *Epeira*) then seize their web strongly, often even shaking it; it is seen that they lie in wait for or will provoke the shakings produced by the prey. It is always the movements of the insect which is caught that guides the spider. It is at each movement that it advances and recognises in which direction it finds its prey.[1] Other spiders, those in angles of walls, for example, do not shake their web, but are content to be guided by the movements of the insect which struggles. So long as it remains quiet, the spider generally waits without movement. When the disturbance is too strong, produced by too big a being, the spiders clear off or rest quiet; or they even cut their webs to let this dangerous animal fall. I have seen them do that also for small insects (as for ants, for which spiders have much fear) when they have recognised them by their movements. But even when a very small, hard insect, as a little weevil, gets fixed in the webs of some large spider, the latter does not always ignore it; sometimes it goes to it, detaches it from the web, and throws it away.

To sum up. Whoever carefully watches spiders in all their varied actions, will see that it is the mechanical vibrations of their webs, the tension, the resistance, which guides them, and not their sense of smell at all. Their vision is extremely indistinct; they see hardly anything but movements, and work as well in complete darkness as in the day. Dugés (*l.c.*) has called the phenomenon of which we have spoken "a pseudo-audition consisting in the perception of mechanical vibrations by the whole body."

The sense of temperature appears as much or as little developed in insects as in ourselves. That is to say, that this sense does not appear to give them more than ourselves any particular knowledge other than that of the degree of temperature, of cold and of heat. Nevertheless one can see, especially in ants, that this knowledge is very carefully utilised for the rearing of larvæ and pupæ, which need a warmth as gentle and equable as possible. Further, ants remove them constantly according to the hours of the day and the seasons, that is to say, according to the temperature, from the lower to the upper tiers of their nest and vice versâ; from parts under the roof on which the sun shines, to those which are in the shade, and the opposite, as Huber (*l.c.*) has already pointed out. With the first sunshine of spring, they carry all under the upper crust of the nest, to return them to the bottom during the night. Under the broiling sun of July they do the opposite, and, at midday at least, carry all to the bottom. The right temperature for each species varies enormously. Whilst various *Nebria* and *Dichotrachelus* live under snow or by the side of it, *Bembex*, *Anthrax*, and some other insects promenade over broiling sand exposed to a midday heat that would almost kill us. Certain insects can survive even (*Fourmis de la Suisse*, p. 432 *et seq.*) a body temperature well below zero. Others, again, die at a less inclement temperature. It is the same for high temperatures.

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[1] This is confirmed by Boys, in his note on the influence of a tuning-fork on the garden spider. *Nature*, vol. xxiii. p. 149.—TRANS.

Sensations of pain are very difficult to distinguish in insects from those of touch. Nevertheless they often give unequivocal signs of discomfort, especially when their antennæ are pinched or when certain corrosive substances or certain strong odours damage their nerve terminations. The same thing is observed when a disagreeable taste, especially a bitter substance (as quinine), has been mixed with their food (Will). But taking everything into consideration, I think that it can be said that pain is much less developed in insects than in warm-blooded vertebrates. Otherwise one could not see either an ant, with its abdomen or antennæ cut off, gorge itself with honey; or a humble-bee, in which the antennæ and all the front of the head had been removed, go to find and pillage flowers; or a cross-spider, the foot of which had been broken, feed immediately on this, its own foot (as I have myself seen); or finally, a caterpillar, wounded near the anus, *devour itself*, beginning behind, as I have observed more than once.

We must, in fine, assign to the domain of varieties of tactile sensibility (or, if it is preferred, of sensations not yet specialised) both the photodermatic sensations and the sensations *of strong odours, or corrosives affecting most varied nerve terminations*, in a word the sensations studied by Graber in his latest works.

CHAPTER VII

GENERAL CONSIDERATIONS UPON THE SENSES—CONNECTION OF THE SENSES WITH THE MENTAL FACULTIES OF INSECTS

INSECTS, then, possess our five senses (save, perhaps, hearing) in a well-differentiated condition and with a specialised energy which we may suppose analogous to ours. The quality of their sight, nevertheless, in divers respects differs widely from ours. Certain among them see the ultra-violet rays, which we do not see. Many insects have, further, a sort of smell-on-contact which we do not possess, and which allows, amongst other things, ants to distinguish their comrades from their enemies, and to perceive the chemical quality of various bodies which they touch with their antennæ, in which the sense is situated. It would appear that their sense of smell, both on contact and at distance, must be relational to space, *i.e.* it must apprise the insect of the relative position of bodies. Have they any other special sense which we have not? This question, so often raised, by Leydig amongst others, is not decided. But the affirmative is possible, for the ultra-violet sight, which we lack, certainly constitutes a peculiar variety of vision in them.

The development of each sense, and of each of its varieties of specialised energy (colours, odours), varies enormously, not only according to families and genera, but even among closely allied species, and among the sexes of the same species. A blind ant, *Eciton Hebschkoi* Mayr, has a male (formerly *Labidus*) which has enormous eyes and three big ocelli. Among the blind workers of *Ponera*, there are some which have large eyes. The sense of smell varies less in allied species. Nevertheless, *Eucera longicornis*, with its immense antennæ, is somewhat closely connected with the bee, in which the sense of smell is little developed. It is true, as has been pointed out by Will (*l.c.*), that many insects have some sense or some variety of the specialised energy of a sense immeasurably developed relatively to the rest. This is evidently the result of the adaptation of a special function which preserves the species.

Amongst these special developments may be mentioned the sense of smell of *Silpha* for putrid flesh and of *Aphodius* for dung, and that of many male insects who seek out the female at great distances by means of their delicate perception of certain odours. It is often enough to place the female of some very rare species on the window to see a male quickly arrive. There is the sense of taste of each caterpillar for its plant or plants. There are, further, the huge eyes of the dragon-flies which serve them for hunting in the air. The hive-bee distinguishes nearly all the colours, which is not the case with the wasp, etc. etc. Nevertheless the importance of these facts must not be exaggerated. Among many insects the senses are sufficiently well balanced. I quote at random wasps, domestic flies, *Formica rufa.*

The actions of insects naturally necessitate combinations of their various senses. But one principal sense is often, as sight is in man, the "directing sense," if I can so speak, that which chiefly directs the insect. Thus in aerial insects, especially in dragon-flies and butterflies, sight plays this part. In worker ants it is usually smell, in spiders it is touch, in caterpillars it is touch and taste combined. Whilst flying, insects which have a good sense of smell do not use it to direct the flight itself, but only to determine the goal of this flight, in the direction of some odour discovered by the antennæ. Thus a wasp discovers honey in a certain direction. It flies in this direction, but the precise details of its movements in the air are all determined by sight, and I have shown above that when deprived thereof a predetermined flight becomes impossible. For the better discovery of certain substances, various insects hover in the air by a to-and-fro movement, as wasps. In apterous insects in general the combination of the sense of smell with touch replaces that of sight with smell, but sight also plays its part.

I have not experimented with aquatic insects. Graber (*l.c.*) found that they reacted to strong odours coming from the air through a thin layer of water. That shows that the substances which he employed were rapidly absorbed by the water. The sense of smell in water, for example in *Dytiscus*, evidently takes place by means of the antennæ by the perception of substances dissolved in the water. Here, then, the sense of smell approaches that of taste, and, perhaps, the gustatory organs play a part relatively more important than the antennæ.

In terminating these studies I may be allowed to say a word as to the connection of the senses with the mind of insects; that is to say, with the functions of their central nervous system. Our idea of an insect conjures up a vision of instincts. But instincts are all closely bound up with sensorial perceptions. In the above experiments I believe I have given several striking examples of this, among others, in the effect of the amputation of the antennæ on the instinct of laying in flies, and on the social instincts of ants. Sensorial perception is, so to speak, the spring which puts the machine in motion. But one must not think that to say this is to say all. Most instincts certainly exist in the latent state, even when the sense which corresponds to them is destroyed. We have seen it well in the amicable or unamicable relations of our ants with cut antennæ. They could no longer tend their larvæ and their pupæ, because they could no longer recognise them.

When one of these ants was perched on a pupa, it did not know it, although possibly it was consumed with a lively desire to possess one. On the other hand, it disgorged honey to an enemy whose movements attracted its attention, but which it took for a comrade.

In a word, if on one side instincts cannot be manifested without the senses, the senses, even the best developed, are of an extremely limited use in stupid insects with little developed brain. One of the most striking facts to demonstrate the matter is furnished by ants. The males are the most favoured sex from the point of view of senses. They have well-developed eyes and long funiculated antennæ. In spite of that, they are the most unoriginal beings, the most maladroit imaginable. They do not even know their nest, lose themselves three inches from the door, are almost unable to distinguish their friends from ants of another colony, are inapt at all work and are fed by the workers. Their sole instinct is that of fecundating the females. The key to the enigma is that their brain properly speaking (pedunculated bodies) is infinitely smaller than that of the workers, although their size is often greater.

The more the intellectual faculties of the insect (and, therefore, its brain) are complicated, the more it knows how to use its senses in a varied way. In what, therefore, do the faculties of the insect mind consist? The scope of this work does not allow me to go into comparative psychology. Nevertheless we can prove in two words that insects have the following faculties :—

1. Purposeful movements, not merely reflex or simple automatic, but very well co-ordinated, almost all prompted by the combinations of instinctive reasoning by the aid of sensorial impressions and admirably adapted to their object. We speak here of the directive acts of the individual and social life of insects, of their "will," very inferior, no doubt, to that of vertebrates, but not essentially different.

2. Often a very good memory of places, of things, and, I was going to say, of persons. It is enough to remember how bees and wasps well know how to find their way without antennæ. One can no longer speak here of a "blind instinct," for the sensorial impression is not there to directly incite them. My wasp without antennæ, quoted above, must, for example, have *recognised* by sight the various objects situated along its road, for, without this, it could not have found its way again through my window to the honey on my trunk, for it could not see the honey until it had entered my room. It was not then direct odour, nor direct sight, but it was the visual memories of objects which made it return to my room. The memory of insects varies much. We have seen that certain ants recognise their companions at the end of several months, and that others have forgotten them at the end of six weeks. I have observed (see above) that wasps have a much better memory of places than humble-bees (*Bombus*), although the sight of the latter is rather better, and we have just seen that this memory is independent of the antennæ. The males of ants show scarcely any trace of memory, and this is the case with many solitary insects, but not with all. Thus a *Dytiscus marginalis* that I had in a bowl, and which I was in the habit of feeding when I returned,

finally became somewhat tame. Instead of flying to the bottom of the bowl when I entered, as he did at the beginning, he started to jump almost out of the water and immediately seized what I gave him, even the end of my fingers. Heretofore tranquil, he began to move when he saw me come in. He must have remembered that it was I who brought him food (I do not believe he distinguished me from another person). I even got to making this aquatic insect eat on my table. Only he instinctively acted as in the water and stretched his front feet forward, which made him tumble regularly on his back, but did not prevent him from finishing his repast in this abnormal position.

If we take note of these facts, we should understand that, when insects find their way, it is not only that they are attracted by the same cause, or that they follow a track without reflecting, but because they make use of their memories. Consequently the sensorial images perceived in the course of their life can be preserved and utilised by the insects, at least by the most intelligent. One fact again demonstrates this. When a plate with honey is placed in a spot in autumn, the wasps, attracted at first by the odour, will return to visit it and eat there. When it is afterwards taken away and replaced by an empty plate, the wasps will return there, to a certainty, even when the honey is no longer upon it. This is demonstrated by Lubbock's experiments and by our own.

Insects, therefore, reason, and the most intelligent among them, the social hymenoptera, especially the wasps and ants, even reason much more than one is tempted to believe when one observes the regularly recurring mechanism of their instincts. To observe and understand these reasonings well, it is necessary to mislead their instinct, as I have shown in my *Fourmis de la Suisse*. Further, one may remark little bursts of plastic judgment, of combinations—extremely limited, it is true—which, in forcing them an instant from the beaten track of their automatism, helps them to overcome difficulties, to decide between two dangers, etc. From the point of view of instinct and intelligence, or rather of reason, there are not, therefore, absolute contrasts between the insect, the mammal, and the man. In the insect, the inherited automatisms play by far the preponderating part, developed and specialised to an unheard of point, and, curiously enough, often coming to produce very analogous effects to that which man has found with his plastic judgment. Let us reflect on the slavery and the breeding of cattle (of plant-lice) among ants. As Pouchet has very well pointed out, instinct and reason do not occur in inverse ratio, the one to the other. The most intelligent insects are generally, but not always, those which have the most varied instincts. In my opinion there is no necessary relation. Water-beetles and ants are relatively intelligent insects. Water-beetles nevertheless do not possess very complicated instincts. Certain caterpillars which have very complicated instincts nevertheless are not capable of varying their methods, and are lost by the least disarrangement of their instinctive acts. Therefore their intelligence is of the smallest. The *Apoderus coryli* has a very complicated instinct, without being also intelligent.

Instinct is reasoning, organised, systematised, automatised. It seems to require much less nervous substance for fixed or instinctive reasoning than for reasoning actual, individual, new, and combinative; these two factors occur in all animals which possess a nervous system, but in the insect plastic reasoning is only a spark which serves as a base for each new complement of its so highly developed instincts. The bird is yet more plastic in its instincts, the dog yet more, and the monkey more than the dog. Woman is on an average more instinctive and less plastic, less combinative than man. And man is, for all that, all stuffed with automatisms. His nervous system has the potential faculty of producing by education, by individual acquired habit, an almost infinite crowd of the most varied secondary automatisms, prepared by often repeated plastic acts. In reality, each human brain only realises a relatively small part of these automatisms called habits, technical skill, learning of all kinds; but this minimum part is relatively immense to the limited instinctive cycle of an insect, so admirably adapted to its special object. It is evidently this potential faculty which necessitates the great mass of the human brain—or rather it is the great mass of the brain which is developed with it, whilst the small brain of insects can only produce in each of them a very small number of definite automatisms of which the perfect adaptation to a very special end makes up for the relative invariability.

Finally, insects have passions which are more or less bound up with their instincts. And these passions vary enormously according to the species. Certain species are extremely irritable and choleric. As wasps, the *Formica rufa*, the *Formica exsecta*, the *Polyerges rufescens*, the ants in general, each to a very different degree, the *Ocypus olens* amongst beetles. Nevertheless certain ants, the *Myrmica latreilli* (*Fourmis de la Suisse*, p. 351), for example, are gentle, peaceful, and timid. The *Carabidæ*, although as carnivorous as *Ocypus*, are but little irritable. The rage of the *Polyerges rufescens* can make it like a mad thing and leads it to kill its own slaves. In my *Fourmis de la Suisse* I have noted the following passions or traits of character among ants: choler, hatred, devotion, activity, perseverance, and gluttony. I have added thereto the discouragement which is sometimes shown in a striking manner at the time of a defeat, and which can become real despair; the fear which is shown among ants when they are alone, whilst it disappears when they are numerous. I can add further the momentary temerity whereby certain ants, especially the *F. sanguinea*, knowing the enemy to be weakened and discouraged, hurl themselves alone in the midst of the black masses of enemies larger than themselves, hustling them without taking the least further precaution. We have observed an analogous temerity among wasps.

When one observes the more stupid species, one no longer recognises passions, apart from hunger, thirst, and sexual appetite. It is thus among male ants, the *Chrysomelidæ*, and the silkworm in the perfect state, in spite of their well-developed organs of sense.

It is curious to note that the intelligence appears much more developed among certain insects in the larval than in the perfect state, as among the *Ephemera* (Mayflies) and the *Phryganea* (caddis), but it is the great exception.

Therefore, when we study the manners of an insect, it is necessary for us to take account of its mental faculties as well as of its sense organs. Intelligent insects make better use of their senses, especially by combining them in various ways. It is possible to study such insects in their homes in a more varied and more complete manner, allowing greater accuracy of observations.

Lastly, I must mention the existence among certain insects of curious sensory organs described by various authors. I merely quote the tympaniform organs in the anterior feet of *Gryllidæ* and *Locustidæ*, those of the abdomen of the *Acrididæ* and the curious apparatus in the balancers of the diptera. But as the object and the functions of these organs are as yet absolutely unknown,[1] I abstain from speaking of them here.

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[1] Considered by some authors (Lubbock, Müller, Hensen, Schmidt) as auditory organs.—TRANS.

CHAPTER VIII

THE EXPERIMENTS OF PECKHAM AND HANDL—FURTHER EXPERIMENTS UPON THE VISION OF ANTS

TWO recent works have just appeared to corroborate and complete my experiments.

G. W. Peckham (*Some Observations on the Special Senses of Wasps*; Proc. of the Natural History Society of Wisconsin, April 1887) has made numerous good experiments on the senses of wasps. Without knowledge of Fabre's experiments on *Chalicodoma*, he has made some very numerous analogous ones on wasps (*Vespa*), and completely denies, as I have done, the mysterious instinct of direction, the *Bee-line* and *Wasp-line* of Lubbock. Wasps at first fly all wrong when they are taken very far from their nest, and only find it in the end by searching. Peckham finds, as we have, that wasps do not hear, that they have memory, that they smell the odour of things they are looking for, whilst they pay no attention to various odours which are strong for man, etc.

Handl (*Ueber den Farbensinn der Thiere und die Vertheilung der Energie im Spectrum*, in Bd. xciv. der Sitzb. d. K. Akad. d. Wissensch., Wien, 2. Abth. Dez. Heft, 1886) enunciates a physical theory apropos of the experiments of Graber on the photodermatic sensations of various animals, starting from the fact that, according to Graber, these animals are divided into two categories, those which love and those which avoid the light. The first seek colours that are in relative order as they approach the ultra-violet. The second avoid them less as they approach the infra-red.

Graber thought he might conclude that the animals in question perceive colours by the skin. Handl is not of this opinion, and expresses himself upon the whole as follows:—

“ Graber's law can be explained without any difficulty if it is granted that the animals experimented upon possess no sense of colour whatever, although they have a sense of light of such sort that the strength of their senses is in approximate proportion to the real strength of the ether vibrations (the absolute light intensity). As, according to the above (par. iii.) discussion, the strength of the vibration increases with the length of the waves, it appears natural that light-loving animals should prefer the shorter waves, *i.e.* the greater strength, to the longer waves, and those that avoid the light should prefer the opposite."

Without touching here the mathematical propositions of Handl, we see that his opinion is identical with that which I have expressed in my work (p. 43) on the photodermatic sensations. It is clear that the method and the opinion of Handl only applies to photodermatic sensations studied by the method of attraction and repulsion, and in no way to colour sight by the eyes shown by Lubbock's method (searching for honey on variously coloured discs which the insect always finds again, even when the place and surroundings are changed).

This summer I have had occasion to remake at Schliersee (Upper Bavaria) several experiments on the way in which ants of the genus *Formica* direct themselves when deprived of sight by varnishing the eyes.

1. Aug. 6th, at 8 A.M., I placed myself at the edge of one of the beaten tracks of a nest of *Formica pratensis*, at seven paces from the nest, at a point where the road of the ants crossed a footpath. I took several ants returning from their aphides with the abdomen (the crop) swollen, a certain sign that the objective of their journey was their nest, and in some I cut off the two antennæ, in others I varnished the two eyes and the ocelli by the method indicated in my memoir. The ants without antennæ ran in every direction, finished by leaving the road completely, then by resting motionless in a corner. The ants with varnished eyes began by behaving in an analogous manner. Several died soon on account of the manipulations which they had undergone at my hands. The ants of the genus *Formica* are both very delicate and very irritable, which makes the operation of varnishing the eyes and ocelli a very delicate one, for they often

burn themselves by ejecting their venom whilst they are held. Nevertheless it is evident that the three which remained in good condition were embarrassed. They made tours and detours in the grass at the edge of the footpath, passing and repassing over the road frequented by their comrades, also turning aside, but returning on their steps, nevertheless without finding the direction of the nest. After a sufficiently long time, while I was experimenting with one of them on a mound of bare earth where the ant road passed (between the footpath and the nest), there came along the first varnished ant which I had left at the edge of the footpath towards the mound, following the high road. I then followed it with attention. It made many wanderings, now above, then below, much more than normal ants. But the more it came near to the nest, the more it went right. Finally it went very well. When it came to turning back it did so only for several steps and it quickly went back in the direction of the nest. I followed it to one of the entrances of the nest, where it went in. I immediately thrust in my finger and caught it again. Attentive examination with a lens showed in the centre of one of the eyes, at the bottom of a little funnel left free in the midst of the mass of black varnish, two or three facets remaining free. These two or three facets entirely surrounded by a high rampart of black varnish could not, in my opinion, have served to direct it. Nevertheless it spoiled the experiment. The other two varnished ants, more quickly discouraged, were cowering under the leaves and would no longer move. I then had to continue my walk.

2. The following experiments were made on August 8 on the path of an ant-hill of *F. pratensis* much longer than the previous one, at forty paces and more from the nest, which was situated in a meadow. The ant path left the meadow to cross a road. On the other side of the road it went along a little footpath, hardly visible, perpendicular to the road and bordered by brushwood (with a little grass between the footpath and the brushwood). The ants passed in the grass or even on the edge of the footpath. I experimented at first in this latter spot, and always on workers returning to the nest with the abdomen full of the liquor from the aphides.

(*a*) I first followed for a space of seven paces a normal worker, for comparison. It went straight, without hesitating or loitering. Once only did it turn back, but only for two or three centimetres, then it again took the right direction.

(*b*) A worker carried a caterpillar to the nest. I removed by a scissor-cut both antennæ. A few rapid steps carried it a short distance towards safety, and it then remained motionless. I gave it back the caterpillar, putting it between its legs, etc. It paid it no further attention and no longer knew how to find the way to the nest.

(*c*) I cut off both antennæ from several workers (usually only the funicles, which is enough, as we have seen). The effect was always the same. They lost all direction, made several circuits, passed across the route frequented by their comrades, paying it no attention, or flying from the latter, and finally always seeking a corner, where they sat motionless.

(*d*) Another worker's eyes and ocelli I carefully and *completely* varnished. Then I put it back on the ant road, at the edge of the footpath, very close to the nest (about forty paces away). It hesitated a little, then took the right direction. But it made numerous wanderings, returned in its tracks, made excursions to the side, almost into the brushwood, or on the footpath. Nevertheless it always returned to the right road (frequented at this distance from the nest by a few workers) and followed it altogether faithfully, despite turnings back or digressions to the side of one or even two decimetres. The intention is undoubted; it wished to return to the nest; but it had infinitely more difficulty to find its way than the other ants. It followed the right track in this manner under my eyes over a space of seven of my paces and thus approached as many from its nest. It then reached the road mentioned above and at first began to cross it very well. But, arrived near the middle, it commenced to diverge from the line followed by its companions and to descend the road. It searched, going and coming in every direction, but lost itself more and more, going adrift and finally descending the road perpendicularly to the line which it ought to have followed. The digression of about one metre from the line to follow was sufficient to lose it. After long fruitless searches it descended the road adrift, getting about seven paces away from the right path, and finished by getting lost in the brushwood at the edge of the way, where, fatigued, it crouched down. We must add that the whole edge of the way was frequented by numerous comrades from its ant-hill, who foraged there. This, added to the absence on the road of an ant path, recognisable to touch, was the natural cause of its loss of direction.

(*e*) I again varnished similarly two workers and put them back, one at the spot whence I had taken it, the other much nearer to its nest. The time was more advanced and the heat increased. They both searched a very long time, returning more or less to the point of departure. It appeared evident to me, by their gait, that when they were on the path of their comrades they perceived it and tried to follow it. They also noted their mistake when they were too divergent, for they retraced their steps. Twice they became involved in the opposite direction, that is to say, in following their friends' path well, but going away from their nest. Finally both, fatigued by their meanderings and their mistakes, ended by squatting under the stones or leaves situated on their comrades' path. One of them was noticed and picked up by a friend, who carried it to the nest after the system of mutual transport of *Formica*.

The result of these several experiments appears at first sight contradictory to my former observations on *Camponotus ligniperdus*, as well as on *Formica sanguinea* and *fusca*, which, the eyes being varnished, guide themselves and carry their pupæ as rapidly and surely to one or the other goal of their receiver as their unvarnished companions (this was especially striking in experiment 45, page 64 *et seq.*). The present experiments prove in every case that sight aids much more in the guidance of *F. pratensis* than I before believed, and that the loss of this sense embarrasses them greatly when they are taken too far from their nest even when they are placed on the road which they know and which they were following an instant before. Nevertheless, on the whole, I have confirmed the fundamental fact which resulted from all my former experiments: without antennæ they are entirely lost; without eyes they can still manage to find their way *if one does not give them too difficult a task*. But ordinarily the two senses help them to guide themselves, and in that I am obliged to modify a little my old opinion which attributes to the ant's antennæ the entire command of the faculty of direction.

If we take account of the following facts, the apparent contradiction is reduced, however, to very little or nothing :—

1. *Formica pratensis* (the *Formica* in general) is one of the ants which has the best developed vision, and which at first sight appears especially to rely on this sense for its excursions from the nest, as I have already several times remarked.

2. Ants of the genus *Formica* have the sense of smell of the antennæ relatively little developed (to this I have already drawn attention elsewhere), and they become lost sufficiently often without their being deprived of sight or any other sense. They are then sometimes picked up by their companions, as one of the blinded ones was in the above experiment.

3. The difficulties to be overcome were great in the last experiments, small in the preceding ones (particularly in experiment 45 which we have quoted). It might be easy for an ant to find its way without eyes in a box, when it is difficult in the open air and far from its nest.

CHAPTER IX

CRITICAL REMARKS UPON EXPERIMENTS MADE SINCE 1887, WITH SEVERAL FURTHER EXPERIMENTS OF MY OWN, UPON INSECT VISION—COLOUR VISION—DISTANT VISION

I. SIGMUND EXNER[1]

WE owe a special debt to Exner for his profound physiological study of the insect and crustacean eye. This masterly study, containing his previous works, modifies certain important points, without making any radical change. Before giving a sketch thereof, I must insist upon a fundamental law which should not be lost sight of, for it underlies all the senses. *The acuity of a sense organ is always—everything else being equal* (as we shall show illustrated in *Copilia*)—*proportional to the number of terminal nerve elements which compose it.* The apparent exceptions to this law (augmentation of the number of elements in larger animals, possible extent of vision in *Copilia*) only tend to confirm it. It appears to me that this has too often been neglected in the theories that have been put forward as to the senses of insects.

Exner has succeeded in discovering and fixing the single direct image formed by the faceted eye of *Lampyris splendidula* (glow-worm), and no doubt more or less clearly distinguished by the brain of the insect. This image is appreciably more distinct than that which he had theoretically supposed, and which I have theoretically figured in the first part of this work (Plate i. Fig. 3). Nevertheless although it is not very distinct, it must not be forgotten that my figure is based upon an image supposed to be formed by three facets only and caused by an extremely small object. Let us say at the outset that Exner asks himself whether the insect is capable of perceiving this image as distinctly as it has been seen and photographed by him. Whilst admitting that it is probable, it must be agreed that this biological experiment can only give an approximate proof, such as that which we have given above, and as Exner has, moreover, recognised.

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[1] Sigmund Exner:—

1. *Durch Licht bedingte Verschiebungen des Pigments im Insecten Auge und deren Physiologie Bedeutung.* Litzber K. Akad. Wiss. Wien. malt. natu. Classe, Bd. xcviii. Abth. 3, März 1889.
2. *Das Netzhautbild des Insectenauges.* Ebenda, Februar. 1889.
3. *Die Physiologie der facettirten Augen.* Leipsic und Wien bei Pranz Denlike, 1891.

The image obtained by Exner in the eye of *Lampyris splendidula* is that of a window situated at 225 cm. from the eye; on this window is stuck a large R in paper with legs 4.9 cm. broad, and through the window a church tower situated 135 paces behind it can be vaguely perceived. In ophthalmological terms this image represents a visual acuity of 6/400 to 6/500 Snellen. Therefore a *Lampyris* will recognise the separate stripes of a barred surface when they are 5 cm. apart, at a distance of 2.25 metres. At the distance of a centimetre it will still recognise stripes 0.22 mm. broad. The distinctness of this image corresponds to the number of nerve elements (in other words to the number of facets, since each facet has a rhabdome with a fixed number of seven cells in this particular case), and Exner adds rightly that other insects and crustaceans with eyes larger and richer in elements give no doubt much more distinct images.

In reply to a precise question put on this subject, Prof. Exner has answered me in the following words: "I can now affirm with certainty that the distinctness of the image increases with the number of facets falling under the same angle of the convexity of the eye (*mit der Anzahl der auf jeden Winkelgrad der Augenwölbung entfallenden Facetten*)."

In spite of these facts, the theory of J. Müller on mosaic vision undergoes, in consequence of Exner's works, modifications of some importance. Once more a profound study shows the folly of premature generalisations, while revealing the complexity and diversity of particular cases. It is impossible for me here to enter into the details of the dioptrics of the faceted eyes; I confine myself to the principal results, referring the reader to the study of the original.

Exner studied fully the index of refraction of the various refracting media of the eye in numerous arthropods. He compares the effect produced according as the animal saw under water or in air, an effect little different, thanks to the structure of the said media of the eye. He proves that the substance of the crystallines is stratified in layers of variable refractive indices in negative progression. By this fact the peculiarities of the cylindrical form which each facet assumes are combined with those of a lens which makes the rays convergent, and Exner gives to this apparatus the name of lenticuloid cylinder (*Linsen-cylinder*). This obliges him to modify his former theory, according to which the rays would have been simply reflected by the walls of the cylinder. I cannot enter into the mathematical calculations, nor into the observations and corresponding verifications made by S. Exner with the help of his brother Prof. Karl Exner. Their general result is that it presents two principal cases: (*a*) The focus of the refracted rays is found at the posterior base of the cylinder (of the crystalline cones), whose length therefore is its focal distance. Then the central rays of the facets become parallel from their exit from the cylinder (towards the retinule), after having formed the image. (*b*) The cylinder is twice as long as its focal distance. Then the reversed image of a very distant object is formed at the centre of the length of the cylinder, and the rays at first leave behind the cylinder as they entered, *i.e.* under the same angle that they formed at their entry with those of another point of the object. It is the effect of a non-magnifying astronomical telescope, focused for infinity.

But in reality the facets of arthropods present very varied combinations of these modes of refraction, which aim at concentrating a pencil of rays thus refracted in the form of a nebulous reversed image of a very limited part of an object situated in the visual field. The collection of pencils of a great number of facets serves to form the large erect image which is perceived.

Exner shows that there are, corresponding to what has been stated, two principal forms of dioptric vision (by refraction) according to the species of insects and crustaceans.

(1) In the first the corneæ and the cones are confined more

or less to the effect of a lenticuloid cylinder (A) of the length of the focal distance. The cones are surrounded by pigment up to their posterior end, which often allows the light to pass only at a very small central point. The sensitive nerve elements are short and come immediately behind the cones. The luminous pencils of each facet therefore react to each retinule separately, and form by their combination an erect image *by juxtaposition* in the same plane situated immediately at the extremity of the cones and tangential or identical to that of the whole of the retinules. This is the case with the eye of a crustacean (*Limulus*[1]) studied by Exner, who has succeeded in seeing its erect image.

But in many insects the visual rods are very long (rhabdomes), and are separated from the cones or crystallines by a transparent tissue (vitreous body) of considerable thickness. In this case the theory of Müller undergoes a great modification, due to what Exner has called the erect image *by superposition.* Here the pigment is concentrated more forward, between the crystallines, whereas the posterior end of the latter is bare. Then the luminous rays are refracted in each facet through the cylinder, having a length double its focal distance (B), thus acting like an astronomical telescope focused for infinity.

Rays which come, *e.g.*, from a source of light sufficiently distant to be considered as giving out parallel rays, are refracted by several facets in such a manner as to become superposed over a certain length of the same element (rhabdome) of the retina; a ray coming from the right part of the object will go to the right side of the image (erect image). The rays leaving a second light will go to be concentrated (superposed) on another rhabdome of the same side as the said second light and so on. In a word, it will be formed into an erect image by superposition of the luminous pencils refracted from different facets. The same neighbouring facets will participate in part in the different portions of the image. This is only possible thanks to the absence of pigment in the posterior thickest portion of the dioptric apparatus. This vision approaches a little to that of vertebrates. I naturally refer to the mathematical proofs given by Exner, as well as to his figures. It goes without saying that this eye uses many more rays than that which gives the image by juxtaposition in absorbing most of the oblique rays.

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[1] Since the French original was written, *Limulus* has been referred to a class of *Arachnida* (*Xiphosura*, a branchiate form) owing to its striking resemblance, even in many points of detail, to *Scorpio.* The relationship thus indicated is strengthened by the structure of the fossil *Eurypterina*, which are to some extent intermediate between these two orders.—TRANS.

But Exner has stated that the image by superposition is only formed in nocturnal arthropods. In the diurnal ones, which are incapable of flight and of guiding themselves at night, the pigment is disposed behind so as to isolate the dioptric apparatus of each facet one from another up to the retina, and thus an image is formed by juxtaposition.

But he has discovered further that a large number of insects and crustaceans possess the faculty of displacing the pigment of their eyes (pigment of the iris) in such a manner that by an intense light it is carried back and absorbs all the strongly refracted rays, only allowing the central rays to pass; whereas in darkness it is concentrated forward between the crystalline cones, leaving their posterior and the vitreous bodies free, so as to utilise nearly all the rays falling into each facet. Exner has even removed one of the eyes of a *Lasiocampa quercifolia* kept in the dark, then exposed the insect to daylight. The pigment of the eye illuminated at the moment of death, and put into alcohol is situated between the anterior part of the rhabdomes and absolutely obstructs all formation of an image common to several facets. That of the eye placed in darkness up to the moment of death is, on the contrary, situated entirely in front between the crystallines (pl. iv. figs. 28 and 29 of Exner). But the animals endowed with this faculty are those which see by day and night. Almost all the insects called nocturnal belong to this category, for they see also by day. On the contrary the true diurnals only have vision by juxtaposition and are absolutely blind by night.

It clearly results from these beautiful observations that the image by superposition has for object the concentration of as much light as possible on each retinal element.

The image of the eye of *Lampyris splendidula*, so clearly photographed and studied in so masterly a fashion by Exner, is an image by superposition.

It goes without saying that there are intermediate forms, even as there are animals which are only partly adapted to night or to day. Exner has clearly shown the mode of development of one ocular form from the other, superposition being derived from juxtaposition.

Both in those insects which see an erect image by juxtaposition, and in those which see it by superposition, the perception of light coming from the same point is never limited to a single facet. The partial "images" of each facet are therefore mingled more or less with those of its neighbours, thus forming a more or less great diffusion circle, which makes the sight less distinct, whilst augmenting the faculty of perception of the displacements of the image, for the smallest displacement of each point consequently stimulates a considerable number of nerve elements. This is, therefore, in relation with the remarkable faculty of the faceted eye for distinguishing movements, *i.e.* displacements. It distinguishes them much better than the vertebrate eye. The latter sees them especially in the peripheral part of the visual field, which distinguishes form badly. In this matter Exner confirms his old data.

Further, the faceted eye has very frequently a catoptric apparatus or *tapetum*, serving to get rid of rays too oblique or those which reach the intervals of facets by reflection. This *tapetum* sometimes gives beautiful reflections.

Another very important point upon which Exner has thrown light is the following: The eye of *Limulus*, and in general the faceted eyes of the more primitive character, are, as has been shown by Grenacher, more related to ocelli or simple eyes. They have a greater number of elements to each facet (14, 16, or more, instead of 4 to 8), and these elements are not welded into a rhabdome. The image by juxtaposition furnished by the eye of *Limulus* is nevertheless an erect single image. But Exner recognised that here each facet begins, perhaps, to be able to distinguish on its own account a partial reversed confused image, according to the theories of Gottsche, being given the greater number of nerve elements. This should be so, for phylogenetic reasons.

To clear up the question, Exner has studied the eye of fossil trilobites. But this eye (that of *Phacops fecundus*) is a link between the eye of *Limulus* and the ocellus. It is large and composed of facets which recall at first sight the eye of *Limulus*. But instead of a crystalline, each facet has a beautiful unique chitinous lens, without cone, like an ocellus. This eye ought therefore to form a reversed image in each facet, the whole being perceived as a large erect image by juxtaposition.

But the spiders have, instead of and in place of faceted eyes, agglomerations of well-developed ocelli which Exner describes as "*hoch-entwickelt*." And he thinks that the sum of the luminous pencils represented by all the reversed images of each ocellus of the spider must form a large erect image more or less diffuse, perceived by the animal as a whole. Here we pass little by little from the faceted eye, and the theory of Gottsche comes more and more into account, as has been seen, for a "facet" which consists of a simple lens necessarily forms a reversed image of objects on a retina situated at its focus.

These facts explain the phylogeny of the two kinds of eyes. A primitive eye, or first transparent spot of the epidermis, in front of a nerve termination surrounded by pigment, first permitted to the animal a differentiation between the sensation of light and that of touch. The multiplication of nerve elements under a simple lenticular cornea produced at first the ocellus, then the eye of the vertebrate. An agglomeration of small primitive eyes transformed little by little into facets, with corneæ, cylindrical crystallines, and nervous rhabdomes, has finished by forming the faceted eye with its special mode of dioptric vision.

Let us pass on to some other details.

Exner has studied the eyes of a great number of arthropods. Certain eyes have an irregular or dimorphic structure. The curvature of the eye varies much. In certain dragon-flies (*e.g. Cordulegaster*) the eye is divided into two parts of different structure. Each special structure has its *raison d'être*, and constitutes without any doubt an adaptation to a special object, an adaptation to which our author believes he can find the optical key in certain cases. The eyes appear almost always as far removed from one another as the dimension of the head will allow. Sometimes they are confluent, having need of all the space.

In *Libellula depressa*, the facets of the upper part of the eye are nearly twice as large and as long as those of the lower portion (the crystallines even more than twice as large). The two parts constitute, nevertheless, diurnal eyes (image by juxtaposition). Exner points out that this disposition makes the upper part of the eye more fitted to see movements at a greater distance, and the lower part more fitted to distinguish the forms of near objects. But the dragon-flies, he rightly says, fly and hover almost horizontally and down, thus seeing especially their prey and their enemies before or behind them, whilst when they see their prey near, they quickly seize it underneath them, and in a condition more or less motionless.

The eye of certain crustaceans (*Copilia*, *Sapphirina*, etc.) is quite unique. It is composed of an enormous and splendid chitinous lens. Very far from it, but attached to it by a muscle and ligaments, is found a crystalline, and behind that a small optic nerve, with a single rhabdome with three cells. Between the lens and the crystalline are parts of the absolutely transparent body of the crustacean. Why should a single rhabdome have an apparatus so remarkable? This appeared incomprehensible to Grenacher. But Exner has observed that the crystalline which forms a whole with the rhabdome is very mobile, and is moved in the living animal symmetrically with that of the other eye, all remaining at the same distance from the lens. In other words, the single nerve element examines one after the other the different parts of the single reversed image produced by the lens; it "tastes" them, so to speak, in a manner analogous to that by which the yellow spot of our human eye tastes or examines, one after the other, the different parts of the image which we see, but of which we only clearly distinguish the point fixed by the yellow spot.

The hypothesis of Exner, in conjunction with his observations, alone explains this singular eye, which forms, it must be acknowledged, an "exception confirming the rule." At the same time it presents a magnificent fact of special adaptation in utilising the transparence of the entire body of the Copepods for their vision.

In the genus *Phronima*, with its immense curved and slender crystalline cones, the extremities of which are absolutely touching the retinules, the formation of an image by superposition becomes impossible. An image by juxtaposition, such as Exner actually admits, is similarly rendered impossible by the curvature and narrowness of the crystallines, which do not allow the dioptric of the lenticuloid cylinder. Nevertheless Exner has been able to convince himself, as much by theory as by direct observation, that the rays are refracted in each facet so as to become strengthened at the extremity of the cones. Here again is formed a single erect image, allied to that by juxtaposition, but more like the primitive theory of mosaic vision of J. Müller. For the eye of *Phronima*, Exner is obliged to retain the views expressed in his first works.

Without any doubt the images furnished by the faceted eyes are deformed. But it must not be forgotten that we ourselves are not conscious of the imperfections of our sight and of our senses in general (witness the colour-blind and astigmatics). The insect whose eye gives it a deformed or nebulous imperfect image has never seen otherwise. It distinguishes animate and inanimate objects and their movements by means of this sight alone, which is its sole criterion of difference. Never realising its imperfections, it goes about its business, its instincts being adapted to its senses and even based upon them, such as they are.

Exner considers the possibility of a kind of accommodation in the faceted eye as very improbable. Nevertheless insects judge distance, even when they have not convergence of the two eyes (which are immobile). Exner believes, however, that the distance of the two eyes and the common part of their visual field (when it exists; among the *Cryptocerus*, for example, it does not exist [see Plate in Part I, Figs. 6A and 6B]) allows by the angle which exists between the axis of the two images a certain degree of stereoscopic vision at short distance. He further points out that, when we close an eye and shake the head, the movement allows us to distinguish the depth, for example, of the branches of a tree, which we could not by remaining motionless. The parallactic movements of near objects are greater than those of distant, which gives an estimation of distance. Thus insects in motion and crayfish with mobile eyes can judge better of depth.

Here I must recall to the reader what I have said above (*l.c.*, p. 41, n. 9.), the rapidity with which the augmentation of distance makes the image of the faceted eye more indistinct must help the insect to judge distances.

Finally, not to mislead us in the complex problems which engage us—for it is a psycho-physiological law of which we ought never to lose sight—*the brain is ruled in the quality of its perceptions by the power of differentiation which the senses supply to it.* It is not therefore purely hypothetical to draw conclusions from a differentiation necessarily proceeding from the structure of a sense to a corresponding faculty of differentiation in the cerebral perceptions. And, similarly, the absence of a sensorial structure must lead to the absence of the corresponding perception (unless it is replaced by another analogous structure, as the faceted eye with its single erect image replaces with certain modifications the reversed image of our eye); further, a supernumerary structure, well characterised in function, must supply a corresponding supernumerary cerebral perception. We shall return to the above subject with regard to the sense of smell by contact situated on a mobile organ, but I wished at first to enunciate the general law with regard to vision.

Before leaving Exner, who has supplied us with the optical basis of vision in the Arthropoda, let us take note that he has discussed certain contradictory hypotheses expressed by other authors (Notthaft, Thompson Lowne,[1] Patten[2]) and has done justice to them. We have already discussed Notthaft above. Lowne suggests that the rhabdome is not nervous and constitutes a part of the dioptric apparatus; he believes he has found a retina further behind. But the rhabdome, seeing its structure, is incapable of supplying the twice reversed image that Lowne attributes to it. Then there is no doubt from the histological point of view that the rhabdome does represent the rods of the retina, organs which we recognise in all eyes.

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[1] Trans. Linn. Soc., 1884.

[2] Journal of Morphology, i. No. 1, 1887.

II. Sir John Lubbock[1]

In his new book, which epitomises his old experiments and those of other authors, Lubbock confirms his former observations and mine on vision, is opposed like me to Plateau, but without entering into details, and adheres to the theories of Exner and Grenacher.

Lubbock expresses doubts as to the conclusions which I have drawn from my experiments on ants with cut antennæ, because "ants when isolated, and especially when suffering, are much less pugnacious than they are under normal conditions."[2] My honoured opponent, otherwise so judicious, is here in error, and for the following reasons:—

Ants with varnished eyes, ants cut in two at the middle of the body, ants from which a single antenna or several feet have been cut off, continue to fight and kill one another as if nothing had been done to them, when they are of different species or colonies. Why should all fighting cease when both antennæ or only the two funicles are cut off? Why does this same double amputation produce, on the contrary, among sisters of the same colony, as does the action of sublimate, a sudden and general war amongst *Myrmica*? These facts are only explained by the loss of the faculty of recognition between friends and enemies by means of contact smell, with which the funicles are endowed. Only—and this is what Lubbock appears not to take into account—this sense of smell is a sense much more complex and relational than ours, and we are far from understanding its riddle.

Apropos of the faculty which ants have or have not of recognising other ants hatched in another ant-hill, but from pupæ which were their own before hatching, Lubbock renews his experiments on *Lasius niger* and maintains the affirmative. I have found the contrary with *Formica*, and that on several occasions. We have worked on different genera. Is that the reason? It is a point which requires elucidation.

For analogous reasons I do not wish to expatiate here on the supposed organs, nor on the faculty of hearing. Lubbock has changed his opinion. Despite the want of direct proofs, he now thinks himself authorised to admit hearing in insects in the sense of Graber, basing himself on the numerous organs of stridulation which have been found among them, and on the presence of tympaniform organs in different parts of the body. The experiment of Will on *Cerambyx Scopoli* appears to him also conclusive. In my opinion these proofs are insufficient. The facts are too contradictory to solve the question. The clear proofs that we have of the existence of the four other senses in insects are wanting here, save for several orthoptera.

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[1] *On the Senses, Instincts, and Intelligence of Animals.* London, 1888, Kegan, Paul, Trench and Co.

[2] *L.c.*, p. 241.—Trans.

Lubbock, on the contrary, agrees entirely with my opinion on the sense and organs of taste, and believes also that the organ of Wolff, in the palate, belongs to this sense. We know indeed to what point the sense of taste and this organ are developed in the bee-tribe, whereas in the *Chalcidites* and *Braconides*, in which the organ of Wolff is almost absent, the course of life requires a very good sense of smell, but not an organ of taste.

For the sense of smell, Lubbock adheres finally to our opinion and confirms its presence in the antennæ. But he believes he has found a certain sense of smell in the palpi. Persuaded, like myself, that the smell of bees, at a distance, is little developed, he does not understand why their antennæ have so great a number of nerve terminations (about 20,000 according to Hicks!), and infers from their presence another sense. But Hicks' calculation is absolutely wrong or due to a misprint. The sensory hair pores of bees are arranged (Hicks demonstrated this himself) on one side only of the antenna, which is very short. It is the median dorsal surface of the last eight articulations of the funicle of the antenna which is the sensory surface of this organ in the honey-bee. According to my approximate estimation, each articulation of the antenna could have 200 to 250 terminal sensory organs (a maximum of 300). It follows that Lubbock and Hicks have put a nought too much and that their total number should be estimated at about 2000 at the most. But Lubbock does not take into account what I have called contact-olfaction, and this sense appears to be well developed in the bee. It is easy to observe that they palpate the stamens and pistils of the flowers they suck, with their antennæ directed one against the other, *i.e.* against the floral organ thus pressed between the two funicles and felt by the sensory surface. It is not a question of touch, but of contact-olfaction, informing the bee of the chemical nature of the flowers.

As to the champagne-cork organs, I have shown (*Études myrmecol.* in 1884, Bull. soc. vaud. sc. nat., vol. xx. No. 91) that they (and also the bottle organs) are wanting in the *Vespidæ* and abound, on the contrary, in the domestic bee. This simple fact at once disposes of the theory which makes them an organ of hearing, as Lubbock would have it, or even of olfaction.

As regards hearing, I am obliged to recall the fact that the internal ear of man and mammals, as well as the acoustic nerve, directs two absolutely different functions. The nerve to the cochlea and the organ of Corti are the only organs of hearing. The nerve to the vestibule and the semicircular canals are the organs of equilibration which probably have nothing to do with audition. The bulbar centres of the two nerves are, as I have demonstrated by experiments done on rabbits (Forel, *Vorl. Mittheilung über den Urspr. des nervus acusticus*, Neurolog. Centralblatt, 1885; Onufrowicz, *Br. Ex. Beitr. z. Kenntn. des Centr. Urspr. des nerv. acusticus*, Archiv für Psychiatrie, 1885), absolutely different one from the other. But there is no proof that the otoliths of the inferior vertebrates, molluscs, etc., correspond to the organ of Corti. The homology with the vestibular apparatus, and especially with the base of the semicircular canals, appears on the contrary more than probable.

These simple facts oblige us to reflect and to obtain excellent proofs before attributing complex organs of audition to insects. The tympaniform organs constitute, perhaps, an unknown sense, very different to hearing.

In what concerns the supposed sense of direction, Lubbock attaches himself absolutely to the opinion which was initiated by Romanes and myself, *i.e.* that it is simply a question of a knowledge of places by sight. He nevertheless avows having been at first seduced by the arguments of Fabre (see above).

As regards sight, and particularly the experiments of Plateau which we are about to see, let the following results of Lubbock be noted: (1) He placed honey on a window and waited 60 hours without a bee finding it. (2) He placed a bee (not used to it, *i.e.* not trained on honey) on a window, at about 250 metres from the hive. It did not return to it (experiment repeated more than 20 times with the same result). (3) Placed on the honey at 25 metres from the hive, in the same way, it regularly returned to the honey, but without bringing companions with it. Never, out of a great number of experiments, did he see bees bring companions on to his window. (4) He placed honey two or three feet from the place where the bees went to forage: they never found it. (5) After long and patient experiments he felt obliged to conclude that bees prefer blue to other colours. But the result of these experiments does not appear to me very clear.

In fine, with the exception of hearing, as to which the experimental proofs are absolutely insufficient, I find an almost complete accord between Lubbock's experiments and my own, save in details of little importance. This discovery has the more value as the critical spirit of Lubbock is specially applied to emphasise divergences of opinion, and as this author is one of the few who have thoroughly entered into and probed the whole question from every aspect.

III. FELIX PLATEAU,[1] FURTHER EXPERIMENTS OF MY OWN

It is with reluctance that I have decided to undertake the criticism of this author, not, indeed, that it will be difficult, but because of the space which it demands, and because it is painful to me to have to bring to light the false conclusions of a colleague whose patience, work, honour, and good faith I esteem. But the considerable confusion that Plateau has thrown on the question which occupies us, in spite of and in part by his long and patient researches, and the fact that his results and his conclusions have been accepted all too easily by certain authors who consider themselves to be very superior to all that has preceded them, demands that we examine the matter closely.

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[1] Felix Plateau:—

1. *Comment les fleurs attirent les insectes.* Bulletin de l'Académie royale de Belgique, 3rd series, tome xxx. n. 11, 1885; tome xxxii. n. 11, 1896; tome xxxiii. n. 1, 1897; tome xxxiv. n. 9, 10, 1897; tome xxxiv. n. 11, 1897 (5 parts).

2. *Idem, Un filet empeche-t-il le passage des insectes? Ibid.*, tome xxx. n. 9, n. 10, 1895.

3. *Idem, Nouvelles recherches sur les rapports entre les insectes et les fleurs.* Mémoires de la soc. zool. de France, tome xi. p. 339, 1898.

4. *Idem, Exp. sur le rôle des palpes chez le arthropodes maxillés.* Bul. soc. zool. Fr., 1887.

5. *Idem, Recherches expérimentales sur la vision chez les arthropodes.* 3rd, 4th, and 5th parts, Bull. de l'Acad. royale de Belgique, 1888.

6. *Idem, Nouvelles recherches sur les rapports entre les insectes et les fleurs.* Mém. soc. zool. Fr., xi. n. 3, 1898, and xii. p. 336, 1899.

7. *Idem, La vision chez l'Anthidium manicatum.* Annal. soc. ent. belg., xliii., 1899.

Before starting I must, to simplify matters, lay down in anticipation certain general theses at which I have long arrived, and which agree, in short, with the results of Darwin, Romanes, Lubbock, and all investigators who have gone deeply into the psychology of insects. But these theses require to be clearly formulated.

(*a*) Granted that there is often a *principal* directing sense, the rule is nevertheless that insects *combine the impressions of several senses for their own guidance.*

(*b*) *Attention* plays a considerable part in the manner in which insects guide themselves. When it is strongly directed towards a goal or an object, they are often profoundly oblivious to everything else, somewhat like an absorbed savant (bee eating honey; ants fighting).

(*c*) The *memory* of insects varies much according to the species. It is connected with various sensory impressions. It is much better than one would imagine a priori in insects with complicated instincts and especially in social hymenoptera, but it is extremely weak in the small-brained forms.

(*d*) As Lubbock and H. Müller have shown, *impulse* plays a great part. Attracted by the sensations of sight or of smell or of both combined, the insect ends by fixing its attention on an object or on an instinctive co-ordinated act, connected with a purpose. When this fact is accomplished, it may be seen to repeat its journeys or other instinctive acts with a rapidly increasing precision. This does not mean that it needs to learn what hereditary instinct has bequeathed to it ready-made, but that to execute with sureness the series of its instinctive acts, a corresponding series of recollections is often necessary to it, *i.e.* of associated and associable sensorial images, not only very clear themselves, but also very clearly fixed in the memory. This is naturally not necessary for acts which do not require memories, as for mastication or copulation. But the complex acts of the social hymenoptera require memory and consequently a progressive fixation of images by repetition, which constitutes habit or impulse, both in the centripetal domain (psycho-sensory) and in the centrifugal (psycho-motor). In ourselves, the same fact is reproduced in an infinitely greater and more complex fashion, and the laws of the fixation of habits or secondary automatisms are the same in the psycho-sensory and intellectual domain (visual and acoustic memories, etc., reading, comprehension of oral language) as in the psycho-motor domain (technical skill). Only in the insect nearly all the habit, nearly all the automatism, is predetermined and fixed from birth by heredity, at least in the details of its principal parts. But, to adapt these mechanisms to each particular case, plastic combinations of memory images are nevertheless necessary. In short, no great combination is required, we admit, because the *portions* of instincts (hereditary automatisms) all ready to act are put in motion with precision when evoked by several sensations, but those sensations are at least still necessary in the lowest animals. Among more developed insects, besides the sensations which are relatively simple, complex perceptions are necessary, which necessarily suppose combinations of recollections between them and with new sensations, for example, the faculty of recognising an object (see Höffding, *Psychologie in Umrissen*: the *perception* implies the *recollection*).

In fine, it is known in psychology that perception is very complex and results from the association of antecedent sensations. It necessarily supposes memory. But the facts oblige us to recognise the existence of perceptions and of memory in insects, at any rate in the higher insects. It is by them that the cut and dried portions of instinct are adapted to each end and combined in a plastic manner. And it is in studying them that we recognise the impulse in each particular case.

(*e*) *Insects have sentiments or emotions* more or less developed according to the species, genera, and families. Rage, fright, discouragement, jealousy are very marked among the social hymenoptera; similarly affection and temerity based on success.

It is necessary to take them into account accurately to judge their acts. Emotional states of the nerve centres are very general in the animal series and are there related with danger, success, defeat, fruitless efforts, pain, attack, defence, as much in the individual as in the society. I have given examples of this drawn from the social life of ants, in my *Fourmis de la Suisse*, and in this work. It goes without saying that we cannot form any idea of the subjective manner in which insects feel their emotions; but the analogy of these conditions and of their motives is such, in the whole animal scale, that one must be incredibly prejudiced to deny it. It may even be said that the primordial emotional conditions are so profoundly connected with instinct, that with ourselves they disclose a very ancient phylogenetic origin, and that consequently there is a priori nothing astonishing in finding them in insects.

(*f*) Nothing is so dangerous as *premature generalisations*, nor as—

(*g*) To *draw illegitimate conclusions from experiments.*

The ground thus cleared, let us say that the frequent errors into which Plateau falls rest in greater part on the fact that he hardly ever takes into account the psychology of the insects, and very often neglects the above factors. To simplify matters we shall refer, in the detail of our criticisms, to the letters (*a*) to (*e*), as well as to the numbers 1 to 7 of the work of Plateau.

1. PALPI.—Plateau (4) still asserts that the palps in insects, crustaceans, myriapods, and arachnids are "organs which have become useless or nearly so, and which these animals can do without, without inconvenience." I was obliged, in confirming the second part of this conclusion, and with the help of several experiments described above, to consider them as simple tactile organs. But the experiments of Plateau give him no right to assert that they are "organs become useless."

As Nagel and Wasmann have well pointed out (see further on), the fact that many insects deprived of their palpi retain taste and smell absolutely does not prove what Plateau thinks he has proved. However, common-sense proves the contrary. Indeed, in certain insects the palpi and their sensory organs are very well developed, whilst they are often rudimentary even in nearly related forms. If their function was rudimentary in all insects, the organ would also be so; this is clear, but Plateau does not appear to appreciate it. But, in his remarkable experiments, W. Nagel has shown that in various insects the palpi serve for a close smell or a contact-smell passing into taste—beyond their tactile faculty, which is the principal, and which they possess in all insects. The experiments of Nagel prove to me that I had not seen all (which was to be expected), and that Plateau is mistaken.

2. VISION IN ARTHROPODS. (5) (*a*). *Vision in Caterpillars.* Here Plateau was struck by a very good idea. Utilising the instinct of most caterpillars of trying to climb a stalk when they are on the earth, he placed them on a horizontal stick and, when they had reached its extremity, offered them a vertical dry twig, 30 cm. long and 5 mm. diameter. He brought this latter up to the point where the caterpillar made manifest and undoubted efforts to touch it (not to be confounded with the blind gropings that it makes to right and left). Tried with fifteen species of caterpillars, the experiments tend to show that they perceived the twig, according to the species, at ½ to 2 cm. distance only, whilst they directed themselves constantly towards the body of the experimenter and to other very large objects, even at 40 cm. distance and more (compare with my observations on *Lasius fuliginosus*). Further, Plateau asserts that the caterpillars did not notice objects in motion at a greater distance than fixed objects of the same size. Being given the fact that they only have 5 to 6 very small, simple, primitive eyes on each side of the head, this observation only confirms Exner. Further, Plateau demonstrates the fact that caterpillars possess a sense of touch, specially by means of hairs, and, in a slight degree, the sense of smell (by offering to the caterpillars fresh stalks of the plants which they seek). If Plateau did not go beyond what these facts say, we should be in agreement.

But because certain myriapods placed under the same conditions do not notice the offered twig, Plateau concludes (1) that it forms in the caterpillar a retinal image and a true vision; (2) that the perception of large masses (his body) at 40 cm. is entirely different and not a vision of the form of bodies in the proper sense. He thinks he has shown thereby that the deductions of Grenacher are false, and that caterpillars must have an ocular structure more developed than has been thought.

It is not difficult to see Plateau's error (8) of reasoning. Let us admit that his experiments on myriapods might be irrefutable, and that these animals only distinguish light from darkness. Grenacher has shown that their rods are horizontal, and it is very possible that their vision may indeed be extremely primitive and inferior to that of caterpillars. But it in no way follows that the fact of perceiving a twig of 5 mm. diameter at 1 cm. distance constitutes true vision, whilst that of distinguishing a man (size about 40 cm., that is, at least, my case) at 40 cm. distance or more does not constitute it. Both cases show indistinct vision of form. Plateau has simply proved that the caterpillar perceived the presence of an object 5 mm. in size at 1 cm., but not that it saw its contours distinctly. After all, I think, without doubt, that caterpillars see a little less badly at close quarters than at a distance, like all the arthropods, and especially those with simple eyes. But from that to the conclusion of Plateau is a great step. He speaks below of the "distance of distinct vision" of hairy and naked caterpillars!

I have not interpreted Plateau falsely, because he says, "At more considerable distances, caterpillars can perceive the existence of large masses; nevertheless they cannot distinguish their nature." That plainly proves that he imagines he has shown that they distinguish the "nature" of a twig 5 mm. in diameter at 1 cm. distance. Let us add that in speaking of distinguishing the "nature" of an object, Plateau implicitly attributes to caterpillars a power of reasoning that these little developed insects have not (*c*, *d*).

(*b*) *Frontal ocelli and compound eyes; varnishing of eyes and section of optic nerves.* Plateau (5) employs two methods, varnishing and section of the optic nerves with a cataract needle. But instead of understanding why I have employed dry Frankfort varnish for varnishing the eyes, by dissolving it rapidly in a drop of chloroform, applying it at the moment when it becomes viscid, and allowing it to dry in a few seconds, he went back to the linseed-oil colour of Swammerdam. This mode of experimenting is absolutely defective, because the eye cannot be covered with a thick even layer, and because, during the slow drying, the insect gets rid of the colour, partly with its feet, partly by knocks against walls and partitions. I have never observed that my insects have been incommoded the least in the world by the last vestiges of the chloroform enclosed in the still viscid varnish.

Then he is "profoundly surprised" to see that the insects whose faceted eyes had been removed or varnished, elevate themselves vertically or in a spiral in the air when the ocelli have been varnished as well as when these latter organs still existed. He has not noted that I have already varnished the eyes of insects which have no ocelli with the same result, which comes to the same thing! However, I have also varnished the ocelli and the faceted eyes simultaneously, and the effect has not varied. In this regard Plateau assigns his observation that insects with varnished eyes raise themselves in the air to a really extraordinary height to the fact that he has become very presbyopic. I may be permitted to observe that presbyopia neither augments the visual acuity at all, nor the distance to which one may see; it only hinders near vision by diminishing the faculty of accommodation, so that a presbyope cannot follow with the eyes an insect to an extraordinary height; the insect is too small for that.

In the course of Plateau's experiments made in a room, the insects with varnished eyes in great part directed themselves towards the window, which was not the case with diptera with divided nerves, as we have seen. That is due to insufficient varnishing, by a method which I renounced from the first. Nevertheless, it is worth noting that five *Eristalis tenax* and several *Calliphora* with divided optic nerves, after having wheeled round up to the ceiling alighted on the walls, whilst the others fell to earth, as in my experiments. This proves that, without seeing and despite their numerous knocks, certain blinded diptera managed to alight, that is to say to hang on without falling. Plateau has operated on diurnal lepidoptera, diptera, and hymenoptera. In general his results agree with my own.

But he believes he has found an important difference between my results and his, because, he says, I launched my insects into the air, and that these threw themselves against the walls, which was not the case in his experiments. Here Plateau generalises inexactly. First, I have not always "launched" my blinded insects, since my cockchafers flew from the ends of my fingers, whilst my *Plusia gamma* and my humble-bee flew all alone. They certainly did not *always* hit themselves before flying high. Then Plateau's experiments with badly varnished eyes do not sustain the comparison. And if our author's pictures be studied, several of his flies with cut eyes are seen falling back on to the earth or hitting against the ceiling or the wall; others fly horizontally in a zigzag (in open air). Finally, the question is one of unimportant individual differences, and the results are the same in their fundamental lines. Nevertheless Plateau, in reconsidering his own experiments, especially on *Bombus* and *Ædipoda*, could not deny that the insects thus blinded had no less a tendency to fly spontaneously than those which saw, and on the contrary more tendency than they to hit themselves against the objects which they no longer saw. The facts are too clear in this regard to allow of doubt.

Basing himself upon his experiments, Plateau constructs the following hypothesis: Blinded insects retain photodermatic sensations (he believes that the transparency of the chitin in many insects is the cause of these sensations), and their love of light makes them fly high, towards the sunshine. The fact that his flies with severed optic nerves flew to the ceiling of the room and not to the window does not embarrass him, because, he says, many insects (these are other insects, the dragon-flies and Rhopalocera, but that does not deter him) fly towards the ceiling even when they have their eyes. The fact that many blinded flies fly to earth or horizontally in the free air has no more weight with Plateau, for he thinks he has proved this to be a question of a derangement of equilibrium provoked by an increase of weight occasioned by the varnish on the eyes. He relies on the experiments of Jousset de Bellesme, who proves that the impossibility of flight in diptera deprived of their balancers rests on a derangement of equilibrium which can be re-established by adding a little weight to the abdomen.

This hypothesis is very unsafe, as shown even by Plateau's pictures. Indeed, for example, of six *Calliphora vomitoria* with severed optic nerves, four always fell back to earth. Here it is not the weight of the varnish which made them lose equilibrium ; and my cockchafers with varnished eyes, much too big for the question of equilibrium to be suggested with them, did not fly to heaven but often to walls, to trees, or redescended after having flown upwards. Nevertheless it is a priori inadmissible that the photodermatic sensations should be adapted to flight. They are appropriate to terrestrial or aquatic animals most commonly blind, and unable to fly. They are slow, and should not be considered visual, but rather as undifferentiated sensations.

Thiebe also criticises Plateau, calling to his attention that in the open air the light hardly ever comes from the zenith, but in cloudy weather from everywhere, and in clear weather from the point where the sun is. In the latter case, the photodermatic sensations ought therefore to make the insect fly in the direction of the sun, which is not the case.

I had suggested to Plateau to experiment at night on nocturnal insects. He did so, and presumed to have proved that, in about twenty-two experiments, nearly all the nocturnal lepidoptera with blackened eyes flew obliquely towards the earth or horizontally. I am not very convinced, because, at night, one can scarcely follow the flight of these insects, and because the blinded insects often start at first towards the ground before setting off into the air. My results, differently obtained, it is true, hardly agree with those of Plateau. But the experiment is difficult, and I cannot come to a positive conclusion.

On the 21st October 1900 I repeated the experiments of Plateau by severing with a cataract-needle the eyes of *Eristalis* and *Vespa germanica* ♂, some in the garden, some in my room. I obtained the same results as he did, and the confirmation of my former experiments. Only *Eristalis* alighted on the walls after having circled to the ceiling, the flight being heavy and insistent. They continued to fly, grazing the ceiling without interruption, or hugging the wall. In this manner it was not necessary for them to see to alight, especially with the very adherent feet of these insects. It is quite another thing to go hurling themselves against a wall or a tree which they do not see when rapidly flying in open air. The dimensions of a room are too small to give the insect time to take a rapid flight. Let us add that the season for *Eristalis* (the autumn) is cold, and that the flight of insects then is slower than in summer, the season when my first experiments were made. The blinded *Eristalis* easily took wing alone.

The wasps, on the contrary, fell to earth regularly, especially in their first attempts. They, however, had no varnish on the eyes to derange their equilibrium. Moreover, these insects do not lose equilibrium for so little, for during flight they use their abdomen as a balancer, and fly even with the third of a wing cut off on one side by curving their abdomen in the opposite direction to restablish the equilibrium.

I repeated the experiments at night, placing my light under the table to avoid lighting up the ceiling. The blinded *Eristalis* partly flew to the ceiling, as during the day, without directing themselves towards the lighted wall, as they ought to have done if the photodermatic sensations had come into play.

It must be added further that in the open air and in the daytime, blinded insects do not alway raise themselves vertically, as Plateau asserts, but very often obliquely.

I had written that "seeing nothing, insects with varnished eyes fly until they hit themselves against an object, which does not happen when they fly high." Plateau calls this "my hypothesis," to which he opposes his own. I had not made any pretension to an hypothesis. I readily agree that this explanation leaves something to be desired, but it has the advantage of being simple and of taking into account all the well demonstrated cases where insects hit themselves and fall (the case of the cockchafers is extremely clear). In the cases where the varnishing is incomplete, it must be admitted that the insect flies to the side where he sees more daylight through the varnish. But in the other cases this explanation does not suffice.

Moreover, another possibility is the following — under natural conditions, the insect finds itself in darkness or semi-darkness when it is underground, in the trunk of a tree, or in a cavern or brushwood. Its small brain does not allow it to reflect upon the cause of its inability to see; instinct impels it to fly upwards to get out of the dark place which it thinks it is in. It will be objected that it does not do so at night, but the solar heat and other circumstances give it the distinctions between day and night, and, further, night is rarely quite dark. Then flight in spiral or zigzag will be objected to, but that is probably caused by the insect being disoriented. However, these are only conjectures, and I believe it wiser not to make hypothetical displays, but to wait for new facts.

To prove that I am wrong in supposing that the ocelli of Hymenoptera, etc., serve for near vision in dark places, Plateau made some *Eristalis*, whose compound eyes he had alone varnished, fly in dark or darkened rooms, furnished with an aperture with a shutter. As the *Eristalis* flew, wheeling about, to the ceiling instead of directing themselves towards the aperture, he decides against my supposition, and declares "that in diurnal insects furnished with compound eyes, the simple eyes are of scarcely any use, and, in every case, only afford these animals very weak perceptions (he means to say sensations), which they do not know how to use," and he supposes "that the ocelli have lost all use in the great majority of insects furnished with compound eyes."

It is not difficult to show that this conclusion is necessarily false. Indeed, if the ocelli had lost all use, and if insects did not know how to use them, these organs would not have taken the enormous development known in certain Hymenoptera, especially in the males of Formicides (see this work, Plate i. Fig. 4*o*, and the frontal ocelli of *Eciton cæcum*, winged male—of which the worker and female are wingless and blind—and which must, therefore, probably seek the female underground). A simple glance at this figure or at any *dorylus* ♂ reduces the conclusion of Plateau to an absurdity To refute me he should observe these insects not on the wing in a room, but on the ground, in their nests or in the cracks in the ground where a very close vision can alone be useful. I agree that this is not easy, but the experiments of Plateau prove nothing of what he wishes to prove. They seem to show, on the contrary, the falsity of his hypothesis of the photodermatic sensations as cause of aerial flight, for the said sensations cannot have taken place in the dark room where the *Eristalis* flew in the air to the ceiling.

Therefore there must be a reason for the ocelli, and their possessors must know how to use them. Only the key to their use as yet escapes us. Nevertheless, the data of Exner, joined to the results of Peckham, Plateau, and myself with spiders, caterpillars, etc., seem to confirm my supposition, made, however, by other authors as well.

How, after all, can Plateau seriously attribute a "distinct vision" to the rudimentary ocelli of caterpillars, and refuse all use to the splendid ocelli of the males of the social Hymenoptera! I had concluded from my first experiment that the ocelli only play a quite accessory part in the vision of insects provided with faceted eyes. I then said in vision during flight. On this point I corrected myself later, for which Plateau does not appear to have understood the reason.

(*c*) *Vision of Compound Eyes* (fourth part) (5). Here Plateau allows himself to be led away by the work of W. Patten (*Eyes of Molluscs and Arthropods*, Mitth. d. zool. Stat. Neapel, Bd. vi. Heft 4, 1886), and commits himself to an hypothesis devoid of all foundation. Patten contradicts not only the works of the best histologists, but the physiological and optical researches so clearly expressed later by Exner, and to which I shall make no further allusion. He denies that the crystallines are refractive media (!), thinks he sees a plexus of nerve fibres between their cells, considers on the one hand the eye with one facet and works from it, on the other, to the thousand images perceived by Gottsche (12,000 to 17,000 in the dragon-flies), which must be further united by the brain of the insect as that of our two eyes is by our brain (we cannot always combine two images, sometimes we see double!). A statement cannot always be accepted merely because it is in print. It would be idle to discuss the phantasies of Patten, and what Plateau deduces from them, especially after the work of Exner recapitulated above.

Nevertheless we will note an important confusion of Plateau. Plateau opposes the opinion that the compound eye is derived from an agglomeration of ocelli to that of Patten, which makes the compound eye an eye of simple origin, secondarily broken up into facets. But if the facts of phylogeny are understood (for example, the eye of trilobites), so well explained by Exner, it will be seen that both hypotheses are equally false, and that the ocellus and the compound eye are both derived from the primitive eye, the first by augmentation of the number of the elements of one of these eyes, the second by agglomeration and transformation of their grouping. The facts are there to prove this. It is sufficient to study the subterranean ants and the series of their eyes of one, two, three, four, five facets, etc., scarcely united, to satisfy oneself of the fact. Further, the aberration of the large worker of the genus *Eciton*, which has one more or less large ocellus developed instead and in place of the compound eye (Plate i. Fig. 5*d*), brings us to the same phylogenetic result. One never sees the eye of an *Eciton* divided into facets, any more than a frontal ocellus. And one does not see in any genus the faceted eye become an ocellus by fusion of the facets. On the contrary, one sees the rudimentary eye of Ecitons, blind or nearly blind, enlarge more and more in the most photophilic species, and that of other subterranean ants multiplied by agglomeration to form the two faceted eyes more and more developed in the most supraterranean species, or vice versa. If Patten was right, direct transitions would be seen from the large ocellus to the faceted eye, without the intermediation of the primitive (rudimentary) eye or of blindness being necessary. But so far, no one to my knowledge has seen these direct transitions, and that is an argument of some weight, if one thinks of the minuteness with which the eyes of insects and the numbers of their facets have been studied by entomologists, as by Grenacher, Exner, and so many others. It will be a question of nothing less than the discovery of a large ocellus beginning to decompose itself into facets, or a compound eye of which the facets tend to fuse themselves (internally, it is understood).

But Plateau accepts from Patten only what agrees with his preconceived idea, by the generalisation of which he scatters confusion over the whole question. This idea is "*Insects do not see forms, or see them very badly.*" Instead of admitting the "thousand images perceived," he concludes from what he calls the histological discoveries of Patten the destruction of the images in the cones, and, without understanding Exner, he deduces therefrom an image "absolutely blurred." Then, even granted that was true, why should nature give herself so much trouble to construct the marvellous apparatus which is called the faceted eye? This is Exner's very judicious remark. And I add, Why does Plateau give himself so much trouble to try and prove that the ocelli are of no use, since the suppression of the faceted eyes disorients the insect, as he himself confirms! If Plateau was logical, he ought to say that the faceted eye as well is not of any great use.

How can an insect on the wing direct itself so well by means of an "absolutely blurred" image? And if it is the sense of smell that guides it, as Plateau elsewhere supposes, how is it that the suppression of this "absolutely blurred" image completely disorients it during flight? Finally, how can it guide itself on the wing by vision without seeing forms or by seeing them very badly?

When Plateau will have explained the web of contradictions in which he is caught, we will accept his conclusions, but not before. These contradictions do not exist in nature, if all the circumstances and all the facts are taken into account, and especially if it is stated that there are insects which have a blurred vision, others which have a better sight, and others which have it relatively good, all according to the development and the nature of their eyes (see Exner); that there are some which use the sense of smell more or less during flight; finally, that the differences of their instincts and of their cerebral development appear again in the way in which they use their senses, independently of the acuity of the latter.

Plateau defends himself against the accusation brought against him of attempting to prove the obvious. We will see if he succeeds therein.

I have reproached Plateau for asking of insects a human judgment by requiring them to distinguish at once a simple opening, furnishing them with a large passage in the shutter of a dark room, from a latticed aperture, with holes too small to allow the passage of their bodies, the amount of light being the same in both cases. Insects fly indiscriminately to both apertures. Plateau deduced therefrom that they did not see forms. I predicted to him that a vertebrate would commit the same error.

Plateau has done the experiment again with birds, and the birds made the same mistake as the insects, save pigeons accustomed to live in a cage and having therefore made the experiment that they could not pass the bars. This result, very significant in animal psychology, has nothing to do, as is seen, with insect vision, and confirms my opinion.

Let us commence by recalling what we have always held—that insects, even those which have the best eyes, see objects in repose much less distinctly than we do (see above). The image of the *Lampyris* of Exner confirms it. Exner has further already shown, in 1875, that the faceted eye was specially and admirably adapted for seeing movements. Our observations have confirmed this, and Plateau is merely working to confirm it afresh. Here every one is agreed. But Plateau forgets that "vision of motion" consists not in the movement of the object seen, but in the displacement of the image on the retina. If an insect *A* flies straight above an uncovered carriage of which all the contents is immobile, at the side of an insect *B*, flying parallel to it, and exactly at the same rate as *B* and as the carriage, no motion of the carriage nor of the insect *B* can be perceived by *A* by means of its faceted eye.

On the contrary, if an insect moves on the wing or on the ground towards an immobile object, the image of this object will be displaced on its retina, and it will see "a movement of the immobile object," as the scenery moves to our eyes when we are travelling on a railway. I ask the reader's pardon for this obvious truth. But Plateau has not taken it into account. We ourselves pay much more attention to objects of which the image is displaced on our retina than to those which are immobile. Still further! If we and the objects remain unchanged, if we had neither eyelids nor movements of our eyes, we should distinguish nothing further at the end of a certain time!

I say without change and not immobile, for the sudden change of colour of an object without any displacement produces a change of stimulation in the image of our retina, as much as a displacement of the said object. Physiology and psychology have proved that if the impressions of a sense (subjectively the sensations) remain a certain time without any modification, they are weakened, then disappear in ceasing to affect us, *i.e.* to be differentiated. In a word *the fundamental sensation of difference is only maintained by its changes in time or space.*

Now an insect remaining a long time motionless before motionless objects, and not changing its position, finds itself in the case suggested. Do not let us ask of it more than of ourselves! It is necessary, therefore, to be exact, to observe the vision of an insect which, after being moved, remains an instant motionless and sees or does not see objects or other insects also motionless. But we have seen that the pairing of the domestic fly gives us a good positive example, the male sometimes leaping several centimetres' distance in flight on to another motionless fly (the errors of sex are frequent), after having been itself motionless for a moment. Peckham has made analogous demonstrations on jumping spiders, correcting my former experiments on this point.

Nevertheless it must be agreed that the displacement in the visual field of objects seen, *relatively one to another*, is a much stronger stimulus, and draws therefore much more attention when they move than when the observer alone moves. What we have just said will make us clearly understand the errors of interpretation in the following experiments of Plateau.

Not allowing himself beaten, Plateau has invented an apparatus which he calls a labyrinth, and which consists of various series of vertical lamellæ, 1 to 3 cm. high, of wood or pasteboard, disposed on a ground uniformly coloured in concentric circles, ellipses, or polygonals, and leaving between them large solutions of continuity, allowing, in a word, an insect to pass without trouble across the labyrinth, provided it avoids the said lamellæ by describing curves.

Arranging his apparatus in such a fashion, that to escape or to reach the light in a straight line (to the window usually), the insects must pass the labyrinth and hurl themselves against the lamellæ (obstacles), unless they recognise their arrangement and describe a sinuous curve, Plateau finally obtained three groups of results:—

(1) Most of the insects (even species with good eyes, as locusts and cicindelæ with cut wings) go straight to the light, hurling themselves against the obstacles, then walking along them to the solutions of continuity or climbing over.

(2) The social hymenoptera, especially the wasps, when they reach the shade formed by the lamellæ, turn round it and thus reach the solutions of continuity, of which they take advantage.

(3) Vertebrates (lizard, tortoise, serpents, ducks, rodents, etc.), without knocking themselves, nor being troubled by the shadow, take a sinuous path with certainty through the free passages, round the obstacles.

Plateau concludes therefrom the distinct vision of vertebrates and the non-perception of form in insects. I agree that the experiment is ingenious and, in all respects, more serious than that of the shutters. Nevertheless, let us consider. How is it that the same wasp that pounced from a metre distant in a straight line on to a black and motionless nail that it mistook for a fly, that the same *Eristalis* which went in a straight line to settle on a flower, that the humble-bee that did the same, deprived of its mouth and antennæ, did not see a vertical wall 1 or 2 cm. from their eyes? Has M. Plateau asked himself this question before drawing his conclusions (*g!*)?

If we take into account the want of plastic reasoning in the insect, the matter takes a very different aspect. In nature, these insects, when they are on the ground, hardly ever encounter any smooth vertical walls. They are accustomed to climb over the stones and brambles, never fearing to hit their hard chitin against these objects, which they usually taste with their antennæ to recognise their chemical nature by contact-olfaction. Further, their brain is too small and too crammed with automatisms to allow them to put the question to themselves, "Shall I pass by this or not?" We know very well that the insect obstinately buzzes against a window, seeks to pass by an opening too narrow for it, crawls up a smooth wall to fall back twenty times without realising the impossibility of its enterprise and without seeking another solution of the problem by going round the obstacle. It is the "stupidity," the "limit," the "beaten path," of "blind instinct"; but that does not prove that the faceted eye has not distinguished the shape of the object. How is it that the social hymenoptera have become more knowing and make a detour round the shadow? Because they, especially the wasps, are a little less limited. And it is these very wasps, which we know by other observations to be the more intelligent, which found their way best in Plateau's labyrinth. The shadow no more hindered a wasp from seeing its way than a gloomy sky, but caused it to turn away from the object which threw it. Plateau asks insects to know that they cannot climb his lamellæ and to be taught by the experiment. It is too much. He quotes the story of Fabre's *Bembex* that returned to the disturbed orifice of its nest, and that no longer recognised its larvæ out of the ground. And instead of concluding, like Fabre, the enormous stupidity (*i.e.* this enormous cerebral incapacity) of an insect in whom the thread of instinct had been disrupted, he infers from it bad sight! He gives the same false interpretation regarding the *Chalicodoma* of Fabre.

At the most one would be tempted, after the experiments of Plateau, to infer a bad stereoscopic vision, an incapacity for judging distances. But such a generalisation would be false. Indeed, the same fly, the same dragon-fly that, deceived by the transparency of a window, hits itself violently against it, will settle with an admirable sureness and exactitude at the end of a small, dry, motionless twig, an object nevertheless inodorous. Without distant vision this would be impossible.

Plateau is astonished that a *Pompilus* could pass 5 or 6 cm. from its prey (a spider) without seeing it. To him it is a proof that it does not see forms. But that happens to ourselves, to men! What hunter never passed a hare without seeing it! And further, our author himself describes that *Bombus* would turn and buzz about his bright blue vest, that *Bombus terrestris*, "manifestly attracted by the lively reddish-yellow of the rhubarb shoots," flies to them, that another *Bombus* is deceived by the white flowers of the rhubarb and flies to them before going to the honeysuckle for which they look, that *Pieris* fly to the white flowers of the Calla which they do not want (deceived by the colour), etc. He tells us all this after having denied the recognition of colours to insects and showed that artificial flowers never attract them!

Plateau rightly points out that with a perfect immobility one can succeed in capturing dragon-flies which have been disturbed, that sometimes they will even alight on the edge of the entomologist's net. It is a proof of their thoughtlessness and of their stupidity, but not of their bad sight. If they did not see the net, they could not alight upon it. But they are careless. Their instinct has adapted them to a temerity ordinarily justified by the rapidity of their flight. They do not know that a net is a dangerous instrument for them. Perhaps, even, they do not recognise it, for want of attention. Nevertheless, when they have been pursued a certain time, they become more prudent and take more notice.

Here I must admit that I expressed myself thoughtlessly in speaking of dragon-flies (see p. 11) and in saying "One might even say that they measure the length of the handle of the net." Plateau retorts, not without some reason, that I seem to attribute to them a capacity for reasoning that they do not possess. Such was not my intention at all, but I admit that my language was too figurative.

(*d*) *Vision of Motion.* To go back to what has been said above. Plateau devotes one whole paper to vision of motion: 5th part (5). Here again he allows himself to attribute to sight what is due to instinct and the want of reason. He studies patiently the following phenomena, well known to every one. Holding oneself motionless or moving with the greatest slowness, one succeeds in frightening insects so little that they will even alight upon one as upon a tree trunk. One can touch butterflies, etc., with the finger, sometimes even flies, by approaching them from behind. Undoubtedly. To that I will reply: a mouse also (whose eyes are not faceted) will even walk on my legs, so long as I keep still. Birds often do the same. Nevertheless a more attentive observation shows that all insects do not act thus. Certain among them, by custom more inclined to fear man, are more circumspect. Others, on the contrary, return in spite of all the movements that one makes, and even in spite of all the blows one gives them, without having a gastronimic object as with gadflies and gnats, and without one keeping still. The dragon-fly which alights on the edge of a net held motionless has no reason by experience to be on its guard, even when one or two unsuccessful efforts have been made to catch it. It meets so few similar phenomena in nature that it returns to the net, since its instinct does not naturally make it distrustful. But when one moves with a net, even slowly, it instinctively forsakes a big being in motion, and is well able to measure its dimensions by vision. It goes without saying that a dragon-fly, not being naturally adapted to be chased by large mammals, is only afraid of them when they move quite close to it.

To prove that in insects everything is only mechanical instinct (instinct is his a priori anti-transformist), the celebrated biologist Fabre expatiates upon the dreadful stupidity of *Bembex*, incapable of recognising the perfidious parasite which flies stealthily after it into its own nest. It has no idea of destroying the larva of this intruder, who eats, under its very nose, the provisions amassed with great trouble by the laborious constructor for its own larvæ. It must, Fabre thinks, see its own larvæ that perish beside those of the thief. One bite would nevertheless suffice for the *Bembex* to kill the inimical worm, which is soft and without defence. I reply: Has M. Fabre considered the Chimila Indian of Colombia, who watches the maggots gnaw his wounds without removing them, and allows himself to die of neglect? Has he considered the European who, seeing his fellows daily besot themselves and die of alcoholism, continues to alcoholise himself? In face of such facts have we so much the right to wax ecstatic over the stupidity of the *Bembex* compared to the wisdom of human reason? The worker continues to work and to economise his pence to a bad end, all to ruin himself in the tavern, just like the *Bembex*, taking no notice of the cheat who ruins his family.

Plateau thinks he has proved that diurnal lepidoptera and dragon-flies see the movement of a large object not further than two metres. I agree that all these insects do not pay attention to distant movements. It is quite natural. Exner remarked that it is the same with small mammals. But according to my observations, Plateau decides too quickly. I am certain of having very often roused the attentions and the fear of butterflies, dragon-flies, grasshoppers, crickets, etc., several metres away, by my movements. I have regularly roused the attention of bees, resting before their hive in cold weather, by shaking a handerkerchief three metres off. It is true that certain active and fearless butterflies will alight again at the place where one has missed them; it is quite as frequent to see them become cautious and no longer to be able to approach them when they have been frightened several times. Plateau only insists on the cases where one may succeed, by a great immobility, in touching them without frightening them. His error consists in deducing therefrom very indistinct vision.

I sum up: In the question of vision of forms, Plateau disputes too much in a matter of words. Really, after much groping, he is obliged to come practically, if not formally, to an opinion which is near to our own. He says that a wasp that mistakes a black nail for a fly cannot see forms. I say that it sees them. I admit that insects do not distinguish very small objects by sight, and that their vision is far from being as clear, especially at a distance, as ours. But those amongst them that have eyes with numerous facets have a retinal image approaching that of Exner's *Lampyris*, much clearer than that which I have depicted (see Plate, Fig. 3). But this really is vision of forms. Plateau has therefore altered nothing of our results. Only he demands that a dragon-fly should recognise on the wing the species of insect which it pursues, and wonders that an insect takes one flower for another, or another insect for its female. He expects of the eye of an insect more than of that of the generality of men.

(*e*) *Experiments with the net.* Plateau (2).—In a curious notice W. Spence (1834) relates that in Italy domestic flies are prevented from entering the houses by placing in the window-frames a net with meshes 25-26 mm. in diameter. This experiment was confirmed in England, and later by Plateau. The latter saw wasps unable to pass through a trellis with meshes 2.5 cm., despite the odour which attracted them. They buzzed in vain before the said trellis, whilst the sparrows passed without hesitation in their flight through meshes 10 by 7 cm.

Plateau explains the matter by saying that the insect, not seeing forms, thinks it finds itself in front of a partly translucent obstacle, but is unable to distinguish the apertures.

Pissot (*Le Naturaliste*, 1. août 1889, No. 58, p. 170, and 1. septembre 1889, No. 60, p. 202) repeats the experiment with a meat-safe with meshes of 28 mm. During thirty-six hours no insect entered. Then the jam under the meat-safe fermented, and several *Calliphora* entered to it. Insects introduced into the meat-safe escaped, some after having made several turns, others directly by passing the meshes on foot or on the wing.

Then Pissot placed a net 60 cm. high, with meshes 22 mm. square, in front of a wasps' nest, at first only covering a portion of the space situated in front of the nest. The wasps arriving were surprised and examined the net. Several alighted on the ground and passed the lower meshes on foot. Others flew beyond the net and entered the nest by the free space. Others, finally, after many hesitations, passed the net on the wing. At the end of a certain time all passed the net, save those which were coming out of the nest, and which used the free space.

Next day Pissot entirely covered the entry of the nest by a net. The wasps hesitated and turned at first, especially those which were coming out of the nest. But soon they passed the net flying, and, at the end of a quarter of an hour, nearly all did it without hesitating. Pissot added that wasps are distrustful and that their preliminary examination of the net was in no way astonishing, but that, when they came to the conclusion that it was not a serious obstacle, they passed through it.

Plateau repeated these experiments by surrounding with a trellis with meshes of 26 to 27 mm. some scabious in flower much visited by insects. Neither *Eristalis*, nor any diptera, nor lepidoptera passed the trellis. On the contrary, several *Bombus* and hive-bees succeeded in so doing. Only Plateau observed that these insects did not pass directly, but first hesitated, then passed with a rush or lightly caught hold of the edges of the meshes for an instant. Nevertheless Plateau agrees that the humble-bees (the largest) alone had difficulty in escaping, and caught hold of the meshes for an instant after having wheeled round. He could not well distinguish the catching hold of the edges by the hive-bees. Wasps and butterflies introduced by him flew directly through the meshes (which he explains by "*the fright of the insect precipitated it towards the brightness of the sky*").

He intercepted afterwards some umbels of *Heracleum* from *Calliphora vomitoria* by means of a net with meshes of *one centimetre*, and declared that the *Calliphora* alighted on the net before entering the meshes. The same observation was made on bees, *Eristalis*, etc., with a cage with meshes of 1 *to* 1½ *cm.*, then on *Calliphora* with meshes of 2 cm.

Finally he repeated the experiment of Pissot with a wasps' nest, but he only made the meshes of his net 15 mm. in diameter. The wasps hesitated, flew in circles, and ended by passing the net, not by direct flight, but by first catching it with their feet to pass the meshes. Direct passage in flight was rare (only twice in twelve outgoings). Several wasps having found means of passing on foot under the net, the others imitated them, and soon all passed thus.

Plateau concludes that his observation does not confirm those of M. Pissot, that wasps do not see form, and that for them a net has almost the aspect of a continuous surface. In the long run Plateau quite admits that the meshes of 15 mm., instead of 22, suffice to explain to a certain point the difference between the result of his net and that of Pissot. But he concludes all the same that the insect does not see the aperture, that its vision is confused, etc.

We draw quite other conclusions from these diverse and interesting data.

First let us state clearly the following facts: A *Vespa germanica* worker has a length of 12-13 mm. and a spread of 22-23 mm. at least. A *Bombus terrestris* worker varies more, but is rarely less than 16-17 mm. long, and 32-35 mm. spread. *Eristalis tenax* reaches nearly to the medium between these two hymenopters. Plateau expects, therefore, such insects to fly straight through meshes incapable of allowing their wings extended for flight to pass. He concludes defective vision from the fact that they strike or catch on the edge of the meshes in order to pass them, even though this catch is of very short duration, in fact, something hardly perceptible for the wasps! Should we do better, in like case, if we could fly? Plateau thinks it very instructive to see these insects "making useless efforts to distinguish an opening when these apertures exist by hundreds." Who told him that the wasps did not hesitate for quite another reason, that is to say, how to avoid striking themselves against all these threads held suddenly in front of their nest? The results of Pissot prove that the wasps pass quite straight, when they are given sufficient room, and time enough to recognise it.

But the experiment is instructive in other ways, of which Plateau does not say a word. It shows once more the relative intelligence of wasps, which, before a new object, first hesitate, examine, then soon find the best way, be it by passing on the wing, when the mesh is large enough, or catching on a little when it grazes their wings, or finding another means (passage on foot, on earth). *Eristalis* do not pass, for want of looking and examining. Humble-bees are generally a little less stupid. *Calliphora*, attracted as always by the rotten food, first alight on every obstacle. They alight on the meshes, therefore, and then pass them on foot. Whoever has seen *Calliphora* throw themselves on to a fly-trap with meshes of 1 or 2 mm., press themselves, buzzing, against its walls, attracted by the food that is within, will no longer doubt. The *Calliphora*, violently attracted by the smell, but altogether too stupid to find out how to overcome a difficulty, as a wasp does, obstinately wears itself out against an obstacle which it seeks to overcome. In nature, where excrements and putrid bodies are often hidden in the grass and bushes, similar pertinacity is often successful with leaves and other flexible or irregular obstacles. At other times, the *Calliphora*, by settling at once, succeeds in insinuating itself into the interstices. Not having comprehended the theory nor the application of the fly-trap, it violently strikes against it after having uselessly sought to enter it by settling on it. Nevertheless, by the force of perseverance, it sometimes manages to pass beneath. Finally, the sparrow folds its wings during flight, whilst the insect can only fly with wings extended, which demands relatively more space to pass.

What is much more conclusive than the experiments of Plateau, is the Italian net with meshes of 26 to 27 mm., hindering the passage of the *Musca domestica*, which are scarcely more than 1 cm. in spread. Here the imperfect vision of the insect appears to combine with its stupidity to bring about this result, if it be exact. I believe that—after what we have seen—

wasps and flies must see the meshes of the net. But they must distinguish the threads badly, that is to say they see them spread out, larger and more misty than they really are. Nevertheless, I beg the reader to recall Exner's calculations on the image of *Lampyris*. The agreement will not escape him. Thus perceived, the whole, new and unnatural to the insect, suffices to baffle it at first. Those alone which are attracted with great violence by a sense (*Calliphora*), those which are persevering, and especially those which know how to get over difficulties (social hymenoptera), return to the charge and end by passing. The wasp especially, which profits a little by its experiences, learns to fly through the meshes large enough to allow it passage when it has seen that this was feasible (Expt. Pissot), proof that it distinguishes at least their centre from their circumference, without which it would strike itself against the threads and very often fall. The more stupid insects or those with weaker memory (diptera) allow themselves always to be baffled, try no expedients, and never succeed, unless when a very violent attraction impels them to alight on the net and seek an entry; then they do as Plateau points out; but it is again the want of reflection and the forgetfulness, much more than the imperfect sight, which keeps them from paying attention to the centres of the numerous passages. It is not sufficient to possess a sense; one must know how to use it. One sees this in man even. I have only to examine, impartially, the results of Plateau himself to be convinced of it.

There are further certain diptera which, however strongly attracted when flying, have not the instinct to try and pass an obstacle on foot. Such are the *Culicidæ*, which alight on the mosquito-net without seeking to pass through its meshes. I do not believe I am wrong in interpreting the matter by the fact that in nature their victims (mammals) are nearly always uncovered. The *Culex* (mosquito) will alight on your trousers and try to pass its proboscis through the stuff, but not to pass under its lower edge, as do, by dint of seeking, fleas, as well as wasps and ants avenging their attacked nests. Attracted by the odour of the sleeper hidden in a mosquito-net, the *Culices* fly straight to him and hum about the muslin, then alight peaceably upon it, without ever trying to surmount the difficulty. Also, in the virgin forest of the tropics, it is sufficient to let the folds of the mosquito-net hang all about the hammock in which one sleeps between two trees, as I have often done. The *Culices* have no idea of passing underneath. I have not experimented on the exact size which must be given to the meshes of a net or trellis for the *Culices* to pass through it flying without striking against it. This experiment would be well worth doing, for, knowing the instinct and stupidity of these insects, it would admit of a certain conclusion on the degree of clearness of their vision. Further, it would have a serious practical value, especially since the magnificent discoveries of Prof. Grassi of Rome on the propagation of malaria by the *Anopheles* (genus *Culicides*). But, here again, account must be taken of the spread of the insect and not of the size of its body. It would be necessary, therefore, to experiment at the outset with meshes of 8 to 10 mm. at least. Nevertheless, from the purely practical point of view, it would be necessary to consider the case where by accident the insect, alighting on a thread, places itself a little towards the interior of the net, and would thus by accident (as Plateau pointed out for the *Calliphora*), on again taking flight, reach unintentionally the inside of the net. That would always be the danger of too large meshes. To judge of the vision it would be, on the contrary, necessary to note the direct unobstructed passage in flight.

(*f*) *Attraction of insects by flowers. Colour preferences.* Plateau (1).—It is well known that Hermann Müller has insisted on the part played by the colours of flowers as a cause of attraction, and has upheld the opinion that certain lively colours of flowers of themselves attract certain insects, *i.e.* that the attraction for such and such a lively colour will tend to direct the insect towards them rather than towards less apparent colours. These preferences of colour thus serve indirectly for the fertilisation of flowers by insects, so that selection will induce the flowers, for this reason, to become more and more coloured. Lubbock has made experiments, whence it resulted that bees and humble-bees had, for example, a marked preference for blue. Let us say, once for all, that this question is *extremely* *complex*, and that the results of observations made without prejudice are not of a nature to confirm in a satisfactory manner the theories of Müller. The results of Lubbock are similarly not very conclusive on this point. It has often appeared to me also that blue was especially apt to attract and to direct bees and humble-bees to a spot; they find honey placed on blue more easily, for example, than if on red. But as insects distinguish the colours on the side of the ultra-violet better than those on the side of the infra-red, the preference might be thus accounted for. White attracts them, in my opinion, as much as blue, everything else being equal. In this question, *distinction* of colours must not be confounded with *preference* for one or another colour. Though the distinction of colours is useful to insects which go on to flowers, to distinguish them and to find them rapidly, the attraction of a special colour will be equally detrimental to them in preventing them from going to flowers quite as rich in nectar or in pollen, but differently coloured, or in attracting them towards flowers or other objects coloured with the hue of predilection, but offering neither nectar nor pollen, or even having poisonous qualities. For these simple reasons, self-evident to the common-sense of a practical entomologist, I have never been able to participate in the theories of Müller and Lubbock on this subject.

I am happy to find myself in perfect agreement with Plateau on this point, of whose numerous experiments (1), all tend to prove clearly what would be expected, *i.e.* that insects direct themselves towards flowers which provide them with the nourishment which they need, and that they find them as well when they are as green as the leaves, as when they are blue, red, or yellow. Inversely, they ignore the most beautiful flowers with striking colours, when they have nothing to give them. Plateau gives himself very unnecessary trouble to show that there are green flowers, and that insects visit them as much as others. Every one knows the first of these facts, and the second has escaped no entomologist, but, in my opinion, his long comparative tables refute Müller. Nevertheless, do there exist any preferences of colour beside this fundamental fact that we have enunciated? This is so difficult and so delicate to decide that I dare not express an opinion.

But Plateau has completed his old experiments on another very interesting point. I am referring to artificial flowers. He has taken enormous trouble to obtain the best and most artistic imitations of natural flowers. To one who knows modern art in this branch this means much, for even man needs all his attention to enable him to distinguish these artificial products from true flowers. Here again I am pleased to confirm Plateau by several experiments that I have been able to make. That which deceives us never deceives insects, or hardly ever, and then only for an instant. The insect passes to one side of artificial flowers without paying them attention, without stopping at them, without hesitating, and goes straight to natural flowers situated beside them, and which we do not distinguish from them! Ought we to conclude therefrom that the colours which we use, and which are not chlorophyllic, are distinguished by insects from chlorophyllic colours? That appears very probable from Plateau's experiments; and I shall believe it until I have proof to the contrary. That which *to our eyes* is a good imitation of colour appears not to be so to the insect eye. These facts will appear less astonishing to us if we remember that among men some are colour-blind, others are artists who render and appreciate colours by many various shades. Then we must not forget that artificial imitations of flowers are made by the help of *human* vision and for it.

But there my agreement with Plateau ceases. Here again he has drawn from his experiments erroneous conclusions. These have led me to repeat several experiments on my own account. Here are, in short, my results bearing on the points in question.

At first Plateau thought that it was the odour and not the colour which attracts insects. He did not take any account of the decisive experiment which I had made (see above), and in which humble-bees with antennæ, palpi, mouth, and pharynx removed returned straight to their flowers without any hesitation. All his deductions collapse before this experiment.

Here are his experiments. Plateau worked on small dahlias with yellow heart and varied colours, visited by numerous insects.

(1) He hid the peripheral flowers of the dahlias with papers of various colours. The insects went, in spite of that, straight to the yellow heart of the dahlias.

(2) He hid the flower. The insects again returned to it, but less often, and sometimes raised the paper to seek the flower underneath.

Plateau concludes that the shape and colour did not attract them. *He forgets that the insect remembered the place where the flower was!*

(3) Plateau hid his coloured dahlias by the help of green leaves of the wild grape, letting the yellow heart alone show. The insects returned thereto as before.

(4) Then he hid the whole flower with two green leaves. The insects returned to it again, he says, as in case 2.

(5) Finally, he masked all the dahlias in a mass with green leaves. The insects returned to them, searched, raised, and found the flower nearly always, especially *Bombus.*

Plateau concludes—

Neither the shape nor the bright colours appear to have an attractive influence. Smell is probably the sense that guides them. Plateau treats as a joke the objection made to him that the insect returns habitually to the place where the flower was.

Persuaded of the falsity of Plateau's conclusions, and having on my terrace a mass of dahlias like those of our author, coloured red, violet, white, rose, brown, etc., and visited especially by numerous bees, I repeated his experiments on September 10th, at 2.15, with the modifications which appeared to me necessary.

(*a*) I first masked 17, then 28 heads of dahlias with a vine leaf fixed by a pin and sufficiently folded round to hide everything.

(*b*) I covered up the yellow hearts alone of four dahlias.

(*c*) I covered the coloured flowers of a dahlia and left the yellow heart exposed by a median aperture.

There remained at the outset 21 dahlias free, then only 10 at the side of those which I had thus masked. Let it be noted that the number of bees visiting the dahlias was very great, sometimes two or three bees foraged together on the same flower. Further several *Bombus* and *Megachile.*

Result.—At first all the dahlias completely masked (*a*) *entirely ceased to be visited by the bees.* These all threw themselves on the heads remaining uncovered.

The bees often flew towards the dahlias "*b*," but generally abandoned them forthwith. Very occasionally they slid under the leaf, which was done especially by *Bombus.*

The dahlia "*c*" was visited like the uncovered dahlias.

After having observed this result, which does not agree at all, as is seen, with those of Plateau, and which was so striking and so general that the ladies and even the children present amused themselves by watching it, I removed the vine leaf which covered a dahlia coloured poppy-red. Immediately the bees returned to it as before.

One of the dahlias "*a*" was, however, imperfectly covered, allowing a rose-coloured petal to be exposed. Several bees, evidently seeing the rose colour, went to it.

Finally a bee, hunting about on the wing, discovered the entrance to one of the masked flowers, and evidently smelling, once quite close, the odour of the dahlia, which was very strong even for us, glided in and discovered the head. From that time it returned to it several times, but *it was always alone and the same bee.* To sum up, hardly any bee searched about the heads covered with vine leaves. The difference is striking, for the others were perpetually visited by a multitude of bees. It is not astonishing that some bees sought for the majority of the dahlias which had suddenly disappeared. It is a phenomenon of memory.

But later the scene began to change. At 5.30 several bees succeeded in their search, found the masked dahlias, and penetrated under the vine leaves to reach them. From that moment others imitated them, and in a short time the masked flowers were in great part visited afresh.

Here it is necessary to observe once again that when a bee has discovered the deception of the masked flower, it no longer hesitates in its after-voyages, but goes straight to the aperture left by the vine leaf. Then a second very characteristic fact is the rapidity with which a bee starts imitating what it sees done by a certain number of others. It is impossible to be mistaken on these two facts. As long as a single bee has discovered something, the others very rarely pay it any attention; when there are four or five at it, imitators follow rapidly.

The next day I was hindered from working at the matter. But the bees visited from that time and up to the 13th September the dahlias which I had left masked by design as much as the others. My deception was quite played out.

Therefore Plateau's observations and inferences are both faulty. First, his dahlias were insufficiently masked, only being covered on the upper aspect; bees flying round a group of flowers must perceive the uncovered coloured sides by their peripheral vision. That appears to me clearly to result even from the figures of Plateau, which show the vine leaf lying flat on the flower. In the second place, his bees had, on this account, discovered his trick sooner than mine; he probably took no account of their manner of acting *at the commencement of his experiment*, or had not noted it. But it is that alone which allows conclusions to be drawn on vision only, independently of memory.

Further, our results confirm the bad sense of smell at a distance in bees.

September 13th. Ten to twenty metres from the dahlias there were in a meadow numerous yellow *Hieracium* and a mass of petunias. The hive-bees went to neither the one nor the other. I took three flowers of petunias of analogous colours to that of the dahlias; I stuck a yellow *Hieracium* in the middle, roughly simulating a dahlia heart, and I stuck my flower thus artificially composed of natural flowers in the middle of the mass of dahlias.

During half an hour of observation I saw a great number of bees, as well as several flies and humble-bees, deceived by appearances, direct themselves onto the flowers which I had made, even alighting upon them several times, but departing almost immediately after having recognised their error, without any doubt by means of smell, sometimes perhaps by taste. Here again the result clearly shows that the bees made their experiments and profited thereby. At the beginning, nearly as many bees flew towards my works of art as towards the dahlias. At the end of half an hour a few bees still flew to them; the greater part having *seen the location* of the false dahlias, remembered it and came there no more. One true dahlia, from which I removed the yellow heart and replaced it by a *Hieracium*, had absolutely and entirely the same fate as the artificial *Hieracium-Petunia*.

But attention should be paid to the following fact: At the edge of the clump of dahlias, at only one of its sides, there was a collection of yellow and white *Chrysanthemum* (allied to *leucanthemum*) with brownish hearts. The bees, humble-bees, etc., which did not care for them, had contracted the habit of flying over, without examining them, and going straight to the dahlias. These insects in their flight passed within some 20 or 30 cm. of the *Chrysanthemum*. I then took a white petunia; I stuck in the centre of this flower the heavy-scented heart of a fine dahlia, and I placed my work of art prominently above the middle of the *Chrysanthemum*. The result was that during half an hour none of the very numerous insects which flew over went to it; all passed without noticing it and went straight to the dahlias of the clump. Finally, at the end of half an hour, a bee having by accident come buzzing round my made-up flower, noticed its smell and alighted upon it. Then a second bee, seeing number one on the flower, imitated it, and so on, so that in a moment this displaced dahlia heart was visited like the others.

Some artificial flowers, placed in the middle of the clump, were ignored with a regularity which would have pleased M. Plateau. Perhaps one or two bees made a swoop in their direction, possibly accidentally, but they never buzzed round nor alighted on them.

As, in my opinion, it is proved that insects, even those which see best, distinguish the contours of objects in a much less perfect and more summary fashion than we do, instead of striving to imitate natural flowers with all artistic care, I myself made, on September 19th, very roughly, several flowers in coloured paper, viz.—

α. A red flower.

β. A white flower.

γ. A blue flower.

δ. A blue flower with a yellow heart, made with a dead cherry laurel leaf.

ε. A paper rose with a dry dahlia heart.

ζ. A green dahlia leaf, by itself.

I placed a drop of honey in the centre of each of these works of art. The observation began at 9 A.M.

During a quarter of an hour of watching, very many bees passed and repassed flying by the side of my imitations in all directions very closely, without paying them the least attention, *in spite of the honey which must have attracted their sense of smell* if Plateau were right.

I went away from them for *a whole hour.* On my return I found the imitation δ empty, that is to say that it had been discovered by a bee which had eaten the honey there. *All the others were untouched.*

Then, with much trouble, I placed the contrivance α very close to a bee that was pillaging the heart of a dahlia. I repeated the experiment four or five times, without the bees perceiving the honey, so much was their *attention* absorbed by the dahlias. At last I succeeded in making the honey touch the proboscis of a bee. It quickly attached itself thereto, abandoning the dahlia, and began to forage in the paper flower. Then I stuck the latter, whilst the bee foraged in it, to a cut twig in the clump, among the normal dahlia flowers, and I painted the bee's back blue.

I repeated this experiment with the contrivance β on a bee which I painted yellow, and with the imitation ε, on a bee that I painted white.

The blue bee soon returned from his hive not far away quite straight to the contrivance α, flew about it persistently, without at first alighting, then went away a little, *saw* the imitation δ, alighted on it and foraged there. Then it returned to the contrivance α.

After that the yellow bee returned to the contrivance β and pillaged there, then went to forage in the imitations α and δ, but, like his blue companion, no longer went to the dahlias.

Then the white bee arrived, which looked for its imitation ε, did not find it at once, and went to forage in several dahlias, as if the recollection of the honey possessed it; it returned to the artificial flowers, without distinguishing them well (*I mean to say without again having well associated the remembrance of their sight with that of the taste and smell of the honey*), then it started to fly towards the brown-hearted *chrysanthemum* and there discovered finally several flowerets of the heart of the dry dahlia of the contrivance ε, fallen directly underneath it. It alighted there and pillaged the honey. I placed the flowerets on the contrivance ε again.

From that time the three painted bees, *but these three only*, returned every instant to the imitations and foraged in them, without noticing the dahlias further. It is necessary to remark here that they discovered by themselves the other contrivances coloured differently to that on which I had first placed them. Thus the blue bee went to the contrivances δ, β, and γ, the yellow bee to δ, α, and γ, the white bee to ε, α, β, and δ. This continued for half an hour. I was able to paint my bees on the thorax, the wings, and the abdomen, without upsetting them, the honey absorbed them so much. None of them found the contrivance ζ, which was lower, a little more hidden, and of quite another shape, confounded further with the other green leaves of the dahlias both by its colour and by its shape. The blue and yellow bees were equally unsuccessful in finding the contrivance ε, more hidden and situated lower, at the edge of the clump.

Let us stop here for a moment. Doubtless M. Plateau would deduce from our experiments that "bees do not see forms and do not distinguish colours." But, notwithstanding, it appears to me that the lesson is clear.

Our bees, attracted by the *multicoloured* dahlias and habituated to them, at first paid no attention to everything that did not sufficiently imitate these flowers *to them*. Our experiments show that the petunias with *Hieracium* hearts alone succeeded in partly deceiving them. When a number of flowers on the dahlias were completely hidden from their eyes, they failed for a time to find them; but a heart or a coloured petal of a lateral floweret sufficed to put them immediately on the track. Even the smell of the beloved honey did not succeed in attracting their attention at several centimetres distance, nor did the smell of a dahlia heart.

But when one has succeeded in attracting the attention of one of them to some honey (placed no matter where, in our case on some shapeless imitations of flowers in multicoloured paper), it immediately changes direction, honey being preferred to the nectar of the dahlia. From that time it abandons the dahlias to fly to the imitations. Nevertheless, a very characteristic thing, it hesitates on its first return; the visual recollection of this clumsy contrivance, quite unnatural to a bee, is not yet sufficiently fixed and associated with that of the smell and cherished taste of the honey. These hesitations I have observed a hundred times with the first return of bees, humble-bees, and wasps in a place and towards an unusual object. One sees it when one has placed some honey or the nest of these insects on a window. For quite a long time they fly backwards and forwards, buzzing up and down three, four, or five windows of the same façade before finding the object sought. I shall never forget the experiment which I made in my childhood in placing a whole nest of *Bombus* on my window, nor the infinite trouble which the poor insects had to find their nest in that totally unaccustomed position; several lost themselves entirely or returned to the position of their old nest. It would be making a great mistake to attribute that to bad vision, for we have seen these same *Bombus* without antennæ or mouth find, in a single attempt and without one single hesitation, any flower in which they habitually foraged. No! here it is a question of quite another matter, of a psychical phenomenon, of an instinct astray. We are asking too much of a poor little insect-brain when we play it such tricks. *We are asking too much of its memory and of the association of its recollections.* My humble-bees (*Bombus*) saw the windows very well. They saw on one of them the cigar-box, covered by a sheet of glass, and enclosing their nest. But was the object there really their nest? Without doubt, before leaving it, perceiving a great change, they did not go away at once, but had fluttered five or six times to right and left in front of the window, thoroughly to fix its position in their memory. This is the instinct of all these insects, every time they leave a newly discovered place to which they wish to return.[1] But once left, our humble bee, after having foraged in various flowers, no longer knows whether it must return to the old ruined nest or to the new one. We cannot picture to ourselves what probably passes in the brain of a humble-bee, but for my part I believe that it first returns to its old ruined nest, of which it has the stronger memories. It finds only ruins there, examines them in vain, flies away again (at least, I believe so), and then its several associations of memories bring it back to the façade and the windows. But during this time its memory, as yet badly associated with the cigar-box in the corner of the window, has been nearly effaced, and that is why it has so much trouble to find its nest in a place so singular, so different from all the objects to which the instinct of a humble-bee is adapted, and to which it was habituated up to that time.

And all these windows, which resemble one another, put it further in error. It examined three, four, before finding the right one.

Still further! Our bees, after having hesitated, did not return, like machines, each to the contrivance upon which it had been placed, but now to one, now to another of those which were in the same region and which simulated flowers of different colours. Plateau would tell us it is because they do not distinguish colours. In every case, then, they distinguished the forms, since the smell had not attracted them before and continued not to attract their companions. I reply thus: They were *habituated* before to visit the many coloured dahlias, to pass from red to rose, to violet, to white, etc., always finding their nectar there. Now, after having found the honey on an imitation, why should they not seek it on another object quite analogous, situated by its side, although differently coloured? They remembered having found nectar in variously coloured dahlias. This fact causes them to take account of colours somewhat. Lubbock, who has shown the distinction of colours by bees, has pointed out most judiciously that to prove the thing it is necessary to *train a bee a long time on one and the same colour*. Then only will it search out this colour alone and not look for honey on any other. But one must have regard for this fact; bees habituated to forage on flowers of various colours jump from one colour to the other without difficulty. That demands some association of memories, but not of a kind of which an insect is incapable, for we observe a multitude of analogous associations in the social hymenoptera. The bee distinguished the imitation from the natural dahlia; that goes without saying and is clearly seen. As long as it had only found the nectar of the dahlias, it paid all its attention thereto and only looked for dahlias, so long as it was able to discover them. But as soon as it perceived that the imitation contained something better, it abandoned the dahlia for it.

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[1] Compare the locality-studies described by Mr and Mrs Peckham in their "Wasps Social and Solitary" (London, Constable & Co., 1905).—TRANS.

Now let us return to our three painted bees which we left at their artificial flowers. There now came by accident, or perhaps because it had seen the painted bees fly thereto, a new bee, which alighted and ate from the contrivance δ on its own initiative. It was just the contrivance which had been discovered spontaneously in my absence by a bee (by itself?). I then painted it with carmine. After that it discovered the contrivance where the blue bee foraged; it drove the latter away and ate there in its turn. And so on. A little *Syrphus* (dipterous insect) discovered the contrivance ϵ by itself; it was the only one. After that my younger son attracted a bee on to the contrivance ϵ. I painted it vermilion. Another bee then arrived spontaneously on the contrivance β. I painted it green. The green bee returned, but to the contrivance δ. Five bees foraged at the same time: the yellow and the green on δ, the blue and the white on β, the carmine on α. But they ranged over all the imitations in turn.

Each painted bee made and remade five to ten visits and more in this manner. It was 12.30 (the experiment lasted from 9 A.M.). The white bee was the only one that knew all the imitations, including ϵ, but always excluding ζ. A new bee followed the white bee flying, alighted on ϵ and foraged; I painted it brown.

From that time two, then three new bees, seeing the painted bees fly in such a number to the imitations, started to follow them there, and I had no longer colours enough to mark them differently. Two or three bees foraged together on the same contrivance. I had to replenish the honey at every moment. I then went to dinner and returned at 1.25.

At this moment seven bees were foraging in the imitation β alone, two in α, one in γ, three in δ, the white bee only was in ϵ. More than half were new bees, not painted, which had followed the painted ones. From this moment a veritable swarm of bees rushed upon the artificial flowers more and more and despoiled them of all that could remain of the honey. At this moment also a bee at last discovered, after more than four hours, and in the midst of the obstruction, the contrivance ζ, which, on account of its different aspect, easily confused with the foliage, had hitherto remained untouched.

Then the swarm, attracted from the hive and turned from the dahlias, became like a pack of hounds on a clean-picked skeleton. The bees sought in vain in every corner of the paper. Nothing more. It was 1.55; they began to spread themselves about and to leave the imitations (become sterile) to return to the dahlias. At this moment I replaced α by a bit of red paper similar to it, and β by a shapeless white paper, also like it. These two new contrivances had never had a trace of honey on them and did not therefore smell of it. Despite that, several bees, still possessed by the recollection of the honey on the imitations, returned to visit these new simulacra. The white bee among others examined the new contrivance B during three or four minutes at least, after having alighted on it. Here smell was absolutely eliminated. It was a question of memories of shape, colour, and locality.

At this moment I removed all the imitations and took them in my left hand to carry them away. Then two or three bees started to fly over my hand and sought to alight on the contrivances which I carried. Here the locality had changed: only the colour and shape of the object could still arouse the attention of the bees. Is this clear enough, and will M. Plateau finally yield to the evidence?—What will he do, in this experiment of the leucophilia, to which Graber and he attached so much importance? How will Plateau and Graber explain that the bees, which, according to them, distinguish neither form nor colour, but only the light and the dark, distinguished in my hand a dark red paper as well as a white paper and a blue one? In my opinion these experiments again demonstrate, as, moreover, did those of Lubbock, that it is rather taste than smell that, assisted by vision, brings bees to honey and flowers. The sense of smell will only serve to guide them and to recognise the right place at two or three centimetres' distance. Therefore—

(1) When a bee has had its attention directed to honey put into clumsy artificial flowers or what not, it returns to it. Its memory calls it back.

(2) At its first return (but not afterwards) it still hesitates a little to associate the recollections of vision to those of taste.

(3) The sense of smell alone only makes it find honey at close quarters, and when its attention is not otherwise too occupied; it plays for the bee a very inferior part to that which it plays for wasps, flies, etc.

(4) Taste is the sense which attracts its attention most, and therefore its will also to the spot where it has found honey.

(5) Vision of form, colour, dimension, and distance (modified stereoscopic vision of the faceted eye) alone directs it in its flight and guides it by means of visual recollections associated to those of taste and smell.

(6) When several bees forage at one spot, they strongly attract by this fact the attention of other bees which then start to follow them. A single bee, especially if it has been attracted to honey at a great distance from the hive, is likely to return thereto alone, but it is incapable of bringing or attracting companions to it (Lubbock). I draw this last conclusion from the experiments of Lubbock, as he does, and my own observations only confirmed it.

At 2.20 my painted bees returned to the dahlias with the others.

We have shown above (whilst discussing Lubbock's work) how bees examine the floral organs with their sense of smell by contact by means of the sensory aspect of their antennæ. Diurnal lepidoptera, *Megachila*, even a *Bombus* male, on the contrary, hold their antennæ raised and motionless during the suction of flowers.

On September 27th I tried an experiment which, though a complete failure, is yet very instructive. An experienced lady painted for me a large band of white cardboard in successive zones passing insensibly from black to white through every shade of grey. My idea was to make a bee find a blue or red paper, stocked with honey, at any place on this band, in order to prove again by another means that it is not merely the light and the dark, but that it is colours which bees distinguish. It is, nevertheless, difficult to eliminate two sources of error: the shadow projected by the edge of the paper, which is difficult to get rid of entirely, and the glitter of the honey itself. Nevertheless, the experiments of Lubbock and myself gave a hope that these little differences might not be noted by the bees. I wished to habituate a bee to the blue, by the help of honey, then replace the blue square by a red square with honey, and then make the bee return to a blue square *without honey*, placed in different positions on the band through the scale of greys going from black to white. If the bee found the blue everywhere, it goes without saying that it is not colour-blind and distinguishes it from light and from dark.

But I tried my experiment eight days after that which preceded, and I had reckoned without the memories of my bees! Scarcely had I placed one or two bees on the blue squares, and had painted them, than they returned to all the squares possible, red, black, white, with or without honey, and the bees of the dahlia clump set themselves to fly towards my band and my squares, taking them, without any doubt, for the repetition of the contrivances with which I had furnished them several days before. And they were not mistaken! I will not pretend that they may have recognised me, for they would have doubtless done the same for any other man, and acted similarly towards the lady who had painted the band of cardboard. But they recognised the whole situation and especially the coloured papers. In a moment a formidable swarm began to pour from all sides onto the band, the squares, my hands, and the board which supported the whole. *The bees even threw themselves onto the empty paper squares.* When two or three were on them, a crowd of others followed. But, when the paper had no honey, all set off soon after, whilst they formed a regular heap on the papers stocked with honey. Finally they even discovered the honey placed under the lower surface of the paper squares, which I amused myself by turning over, for, when they passed over it in their search, the smell made them stop, palpate, and finally lift up the edge of the paper. Their vision made them recognise, thanks to the shadow of the edge or to reflections (the sun was shining), *even a white square without honey on white paper, and a black square on black paper*, although with more difficulty. The papers were from 4 to 4½ cm. square.

I then cut the antennæ of two bees painted green and red. These bees, after having foraged, returned to the blue papers, the green one even onto the bit of blue colour in the colour-box in which it had not been able to go previously (I had placed the box open, on the grass, at several centimetres from the papers).

The experiment, therefore, completely missed its object, but it proves that the memory of bees lasts several days, and that, if one is not prepared to take this into account, one is involved in false conclusions. It would be possible, nevertheless, to repeat the trial with a chance of success, by habituating a bee to blue or another colour far from its hive, without having made any experiment before with it and its companions, and in eliminating all play of shade by the use of a diffused light and the exact application of the squares of coloured paper to their background. I beg the reader to compare the results of the unsuccessful experiment of which I have spoken with those of my previous experiments, made on the same bees, by means of ordinary artificial flowers or contrivances of painted paper, and especially with those of Plateau, obtained with the help of artificial branches of apple-blossom (see below). I know no better way than the use of this comparison to prove that insects with relatively developed brain are not solely attracted or repelled directly by the stimulation of their senses, but that they have recollections of their sensations and associate them, that is to say that they have, besides the sensations, faculties corresponding in their chief features to our attention, memory, and perceptions of objects.

Let us return to Plateau (1, 2nd part, 1896). Darwin having believed he had proved that the blue petals of *Lobelia erinus* attracted bees and that they no longer returned to these flowers when the petals were cut off, Plateau repeated the experiment with *Eristalis* (diptera). His results may be thus tabulated:—

	Intact Lobelias.	Lobelias with cut petals.
Visits with sucking . . .	33	25
Visits without sucking . .	29	16

But the figures take another aspect, if one takes into account the details of the experiment with due reflection and comparison.

First experiment, 14th September, from 9 to 10. Untouched Lobelia, 21 visits. Mutilated Lobelia, 9 visits.

Second experiment, 14th September, from 2 to 3. Untouched Lobelia, 7 visits. Mutilated Lobelia, 7 visits.

Third experiment, 16th September, from 11.0 to 12.30. Untouched Lobelia, 34 visits. Mutilated Lobelia, 25 visits.

The intact Lobelias were placed in one pot, the mutilated ones in another. Let us add that the *Eristalis*, *Vespa*, *Syrphus*, etc., which visited the Lobelias without petals have a good sense of smell, much better than that of the bees observed by Darwin, that the mutilation of Lobelias facilitates the sucking for *Eristalis*, and that a *Vanessa* and a *Pieris* which had been there would have only followed on seeing the other insects. But what we see is that, *to commence*, and *in spite of the general visual similarity of the two pots*, with the exception of the blue petals, the insects went more than twice as often to the intact as to the mutilated Lobelias! Once they had recognised the stratagem, they acted like my bees with the masked dahlias, and the visits were equalised. Darwin would have experimented probably with more judicious precautions, and it is this which explains the difference between his results and those of Plateau.

Then Plateau worked with bees which were visiting *Œnothera biennis* with beautiful yellow petals. On September 3rd he cut the corollas, only leaving the stamens. I give the results in his own words:—

" The bees visiting the plant flew in every direction, towards the faded flowers, towards the buds, even onto the fallen petals on the ground, which they examined with some attention by walking over them ; nevertheless, *they only alighted to forage on the mutilated blossoms deprived of corollas*." (The italics are Plateau's !)

And Plateau concludes that it is smell and not vision which guided them !

Is it possible to prove better to oneself the contrary of what his experiment says ? That bees do not forage where there is nothing, is obvious to a child. But that they should seek their cut flowers, wherever they perceived them, by their bright yellow colour—the debris that Plateau had taken care to let fall on the ground before the plant, better to put himself in the wrong—that they should see the dry rudiments or the buds on the plant—this agrees so admirably with our experiments that I pass no comment. The bees sought, and, finding nothing on what was most gaudy, went to the stamens which remained on the calyx and were rewarded. Plateau thought that the visit to the fallen petals was due to their being impregnated with scent. If he had followed his experiment longer, he would have seen that at the end of a certain time, after having recognised that there was nothing on the said petals, the bees would have ceased to visit them. Other experiments of Plateau himself contradict, however, his erroneous opinion on the sense of smell in bees.

Plateau repeated his experiments with coloured bindweeds, *Delphinium* and *Centaurea cyanus*, with analogous results.

Nevertheless the *Bombus* ceased to go to *Antirrhinum* (snap-dragon) from which he had removed the corollas. He explains this, he says, because the Digitalis flowers have their orifice below and the *Antirrhinum* above, but closed, and that hymenoptera always attack these two species of flowers from below up. But *Antirrhinum* cut has the corolla directed upwards, and this is, according to Plateau, the reason for which the *Bombus* no longer visited them.

One must be on a very false track to seek an explanation so incredible for a fact so simple. In the first place the *Bombus* did not fly towards the *Antirrhinum*, in my opinion, simply because they no longer saw them and were attracted elsewhere. Therefore, according to Plateau, who does not believe in vision for forms, nor in the reasoning of insects, it follows necessarily that the said *Bombus* must have *judged at a distance, on the wing, exactly the shape and the position of the orifice of the mutilated flower, and must have drawn therefrom the conclusion that they could not enter there because of its superior and not inferior position!* I confess that here our author goes beyond my understanding, the more because the *Bombus* forage from above in a crowd of flowers, He suddenly makes these insects past masters in geometry, distinguishing subtleties of form at great distance.

"To refute beforehand all explanation in which set habits will be made to play a part by insects," Plateau then worked on June 5th, on the umbel of a rare *Heracleum* (Umbellifer), a single stalk in his garden, and springing from seeds brought from a distant botanical garden. He covered the single expanded umbel with a large and with several small rhubarb leaves. In thirty minutes he verified seven visits of bees (3) and other insects. The bees first alighted on the rhubarb leaves, walked about there, explored, and sometimes got as far as to reach the umbel below. Plateau believes that the smell had attracted these insects to the umbel. He has not for an instant the idea of thinking that it might be the recollection of voyages that they had made there the previous day. Hence his series of wrong conclusions. June 11th he repeated his experiment on five umbels which had expanded since the former date, verified in an hour and a half forty-five visits there of insects (odynera and diptera) which without any doubt had come to know these umbels from June 5th to 11th. He drew therefrom the same erroneous conclusion.

Perez (*Notes Zoologiques*, Arch. Soc. Linn., Bordeaux, 1894) had placed some honey in the scarlet corollas of *Pelargonium*, which bees do not visit in the normal state. Once the honey was discovered the bees visited the *Pelargonium* so thoroughly and so much that the red colour of the *Pelargonium* was associated in their memory, and that afterwards they visited numerous *Pelargonium* without honey, only leaving them after being assured that they would find nothing there.

To refute Perez, who, as has been seen, is in agreement with us, Plateau (1, 3rd part, 1897) repeated his experiment ***on a border*** of red *Pelargonium* (the italics are mine). He placed the honey on the *Pelargonium* at one point of the border, and simply declares that these were the only ones visited; whereas, *save for several exploratory flights* (notice Plateau's confession), the remaining twenty-five plants in flower were neglected by the bees. Why did Plateau choose a border instead of putting honey in certain flowers of the same plant and not in others? The border forming a line, it was easy to foresee that the bees would not go seeking on the portions of the line where they had never found anything, but simply at the point where they had been given honey in plenty.

He has not, therefore, refuted Perez.

Plateau made insects cease to visit by suppressing the nectariferous part of the flowers, and re-established the visiting by putting honey there. That goes without saying, and it is the story of my painted paper contrivances.

But it would be idle to follow into the details of other experiments which prove nothing for reasons which I think I have sufficiently established. He gives himself very needless trouble, as we have said, to prove that insects visit green flowers as others, and that they visit nonnectariferous flowers (called anemophila, or fertilised by the wind, in opposition to entomophilous flowers, or those fertilised by insects) when honey has been put there.

Artificial flowers.—Plateau returned to these in 1897 and made an experiment which, in my opinion, sums up the whole question and, with exceptional accuracy, marks his fundamental error. C. E. Bedford (*The Entomologist*, xxx. No. 410, p. 197, July 1897) had seen a white butterfly (*Pieris brassicæ*) alight on the bouquet of artificial lilies of the valley in a lady's hat. Plateau says that the *Pieris* had done this by mimetism, intending to alight on a white surface. He therefore agrees that the *Pieris* saw the bouquet white. He adds that, if artificial flowers attracted insects, a swarm of these animals would fling themselves upon the hats of our beauties in all the public gardens, and he is right. If the swarm of insects does not do so, it is doubtless because they distinguish these moving contrivances from true flowers, and that, when by accident they happen to fly onto them, they find nothing to eat there.

Then Plateau placed some honey in some artificial *Myosotis*, and observed that the bees did not visit them more than those which had no honey. Then, on April 30th, he suspended on the most exposed branches of an apple tree in blossom four twigs, each carrying a bunch of artificial apple blossom, imitating the natural flowers of the tree remarkably well, having loaded each artificial corolla with honey. He watched for an hour and a half. The apple tree was visited by numerous bees, diptera, and some *Vespa* and *Bombus*, but in small number. "*During the whole of the time the bees paid no attention whatever to the honeyed artificial flowers; they received only a very short visit from a Vespa, and were only visited a little longer by two flies.*" To make sure that his honey was good, Plateau put some on the natural apple-blossom, where it was greedily eaten by the bees. The experiment was repeated on May 1st, with the same result. Nevertheless Plateau noted several times short flights of inspection towards the artificial flowers, both honeyed and not honeyed, on the part of bees, lepidoptera, etc. But the insects did not alight.

He rightly concludes that the insect distinguishes the artificial from the natural flower, but wrongly that the artificial flower "repels" it. I have proved the contrary by my experiments related above.

What Plateau does not conclude, is that "*the bees did not recognise the honey in the artificial flowers by smell in their rapid flight past, whilst two flies and one wasp did recognise it.* These facts are the exact confirmation of my experiments. If Plateau had himself placed one or two bees on the honeyed artificial flowers, as I did, he would have come to the same result as I, instead of plunging more deeply into error. Further, in this matter, Plateau passes my experiments and those of Lubbock on colour-vision in silence.

He repeated his experiments on honeyed artificial *Digitalis purpurea*. No hymenopter occupied itself with them, but diptera visited them actively and foraged among them. Humble-bees nevertheless swooped towards these contrivances, examined them, but did not alight on them. Plateau does not know how to see the difference between the good sense of smell of the diptera and the bad sense of smell of the bee-tribe. According to him artificial flowers made with green leaves, and honeyed, on the contrary attracted hymenoptera. My experiments quoted above give the perfectly simple explanation of these various facts, and I hope that the reader will be sufficiently edified to allow me to pass in silence the remainder of Plateau's interminable experiments. We shall find nothing new in them.

For the same reason I shall not enlarge upon the researches of Herm. Müller, Bennet, Bonnier, Gratacap, Christy, Bulman, Scott Elliot, Delpino, Küntze, Knuth and Plateau (6) on the truly hair-splitting question regarding the possibility of insects having *preferences* for certain colours or not. Here I am in agreement, as I have said, with Plateau (and Bulman). What is astonishing, is that so many authors can waste so much ink in proof of the obvious, clearly summed up by Bulman when he says "it matters not one iota to a bee whether the flower is blue, red, pink, yellow, white, or green: so long as there is honey, that is sufficient" (*Nat. Science*, xiv. No. 84, Feb. 1899). Only: *The fact that any colour does not attract specially by itself some insect is no proof that it cannot distinguish other colours.*

The last conclusions of Plateau (6, 1899) are somewhat curious. He begins by declaring that he has "never said that insects do not see the colours of flowers; that would be absurd" (*nevertheless*, in 1, first part, p. 472, he puts as title: *On the so-called distinction of colours by insects*).

Then he adds that the differences in the quantities of reflected light or in the refrangibility of luminous rays transmitted or reflected by the transparent media can explain the results hitherto obtained.

And finally he pretends that the question to be solved is: Do the insects which visit flowers allow themselves to be guided IN THEIR CHOICE by the colours which these flowers present *to the human eye.*

To this I reply, from the preceding works of Plateau, and from that which was connected with the theory of Graber on photophilic and photophobic phenomena, it must be concluded that he considered insects as absolutely colour-blind for every colour, *i.e.* distinguishing the intensity of the light, but making no *specific* difference between the length of their waves or the refrangibility of their rays. Indeed, it is precisely these last differences which make us distinguish colours, save the ultra-violet, for which the normal man is colour-blind. Soret has given the reason for it.

I protest against the manner in which Plateau now puts the question. I do not believe any more than he does that insects see subjectively colours as we do, and I believe further with him that there are objective differences in the manner in which their eyes and ours are stimulated by the different forms of light, *i.e.* by colours and their shades.

But the experiments of Lubbock, of Peckham, of other authors, and my own indicate that certain insects distinguish not only flowers, but coloured objects, by their coloration, *i.e.* by the kind of refrangibility of the luminous rays which they reflect or transmit, and recognise them in this particular when the other senses are eliminated, and even when the said objects are found surrounded by light of the same intensity. Now, this is what a colour-blind man cannot do. I have seen two colour-blind persons unable to perceive at one pace distant the red scarlet flowers of a *Cydonia japonica*, a shrub with shining green foliage, and which other people saw at 59 metres. This is a reply to Plateau, who assumes that it is difficult to find two different colours of approximately equal luminous intensity.

In saying that bees distinguish colours, *we have never wished to assume that they see them exactly as man does*, and so much the less, since I have already emphasised, all men do not see them absolutely the same. Therefore I can adhere to the last version of Plateau in this respect, having myself confirmed the fact that insects which I have observed distinguish artificial imitations of flowers where we do not distinguish them.

Finally, Plateau (6) arrives at the conclusion of Bulman, which is also mine, but he attributes to Exner an opinion which is not his, in making him say that even at several metres' distance *the* flowers cannot be seen by *the* insects, except as *absolutely vague* spots (fault *f*). Let us say: in a fashion more or less vague or distinct according to the size of the flower, the distance, the number of facets in the eye, etc.—then we shall say what Exner says and what I say with him.

Distant Vision. Functional Blindness by Absolute Rest of Vision

Since Plateau repeats at every opportunity that insects only see clouds, fogs, spots (which he describes sometimes as coloured, after having expressed doubt as to the distinction of colours), etc., it is necessary to consider a little more closely the question of their distant vision.

Let us start subjectively from our human vision, and let us state in the first instance that the fact that the normal emetropic human eye cannot distinguish the leaves of a tree at four kilometres, nor the windows of the body of a building at twenty-five kilometres, does not imply that it sees the said tree or the said building as a shapeless spot or a cloud when the weather is clear.

Objectively, the image of the *Lampyris* photographed by Exner shows us at 2 m. 25 cm., fairly distinctly, the legs, 4.9 cm. thick, of an R, and at a hundred and thirty-five human paces a church with its tower. Exner adds very rightly that the photograph and its reproduction have made the image further lose its distinctness. Now the church is misty, it is true, but the general form of its tower and the roof of the body of its building can be distinguished very well. The windows are scarcely perceptible, but the wall can be distinguished a little better than the roof. For the tiny *Lampyris* at a distance of 135 paces this is not at all bad, and this degree of clearness is perfectly sufficient to explain to us the way in which insects guide their flight in the air, especially when they have better eyes than *Lampyris* and distinguish colours. To see more distinctly, it has only to approach flying and help itself further by the sense of smell. *Similar forms of objects, especially coloured, suffice to fix memorial images qualified to make them recognise their way in the air, for in a space of* 135 *paces numerous images of objects suc-*

ceed one another, become more clear at a greater proximity,[1] *and suffice, by the association of their sequence in space, to orient the insect.*

It is undoubted that the social winged hymenoptera orient themselves in this manner. The *Chalicodoma* of M. Fabre (which, carried three kilometres away from their nest, marked with colour, then liberated, first flew to a certain height, hovered this way and that, then went off in the direction of their nest, where they arrived in twenty minutes) gave a clear and distinct proof of what we are advancing.

My bees and humble-bees with cut antennæ, and even with the mouth and pharynx further extirpated, which returned to forage in the flowers or to the honey, the bees with only the antennæ cut, which returned even several times following, after having returned from disgorging their honey at their hive, prove beyond question orientation by the vision of compound eyes only, by the help of visual memories. Indeed, we have demonstrated that the presence or absence of ocelli makes no alteration in orientation in flight.

Therefore if great objects moved at a distance do not ostensibly attract insects by vision, and do not further frighten them, it does not at all follow that they are not seen.

Let us remember that vision of movement, which allows the possessor to pursue flying a small insect and to capture it, necessarily implies an approximate visual estimate of its dimension ; that is to say, therefore, of its form.

Finally, we have seen that a complete absence of relative changes and displacement between the object seen and the eye which sees causes at the end of a certain time a cessation of all possibility of sensation. This occurs undoubtedly during more or less long intervals in motionless insects, and explains their apparent apathy, from which the movement of objects awakens them.

I believe I am here on the track of a very important factor of comparative psychology, especially in that of insects. Since their small brain is not capable of any great internal work of thoughts awakening each other by association, its activity must be perpetually kept on the alert by the activities of the senses or of the movements of the insect, in order not to go completely to sleep. When an insect is motionless, with its antennæ folded, it must therefore be in a sort of slumber, so long as neither a shaking, nor a breath, nor a strong odour, nor above all the motion of surrounding objects, especially of living beings, stimulating its retina, come to shake off its torpor. The observation of insects, of their life, and of their actions, appears to me to confirm absolutely this a priori datum of psychophysiology. With resting ants, in their nest, the fact is patent; it even takes a quite noticeable time to arouse them thoroughly. The absence of eyelids, accommodation, and mobility of the eyes tends to produce a visual apathy which may be called functional blindness.

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[1] We have seen that this rapid augmentation of distinctness of contours must necessarily aid them to judge distances, thus partly replacing our accommodation.

In man, on the contrary, the movements of the eyes, of the eyelids, and of accommodation render a similar phenomenon of functional blindness impossible, so long as the eyes are open. But, in considering the vision of insects, we must take account of this fact, which seems to me to have been too much neglected.

Résumé and Remarks

I must make an excuse for my long criticism and my long series of control experiments, as much to M. Plateau as to the reader. But it was necessary. In using the experiments of M. Plateau himself to show the errors of judgment that he draws from them, I fully render homage to his scientific honesty. And it is precisely this honesty which has allowed us to follow the author step by step, and to pick up, by the help of his faithful narration of facts, the thread of their actual connections and their agreement. Thanks to this our study will not have been a sterile polemic, for it has brought us to see more and more clearly into the very interesting question which occupies us.

In recapitulation, we see that the facts are very complex, and this is why I abstain from general conclusions on "all insects" seeing or not seeing "forms and colours, etc.," for such generalisation would necessarily be false. If one wishes to understand it, one must take the trouble to follow the details.

Nevertheless I am constrained to repeat that Plateau's interpretation of his so-called *non-distinction of forms* among insects, after the restrictions which he himself has gradually introduced, finally approaches more or less to the opinion of Exner, which has always agreed with my own. The greatest error *of fact* into which Plateau falls, is that by which he attributes what really belongs to vision in certain insects (in bees in particular), to their sense of smell. Nevertheless, in his work No. 5 (5th part, p. 62), Plateau finally recapitulates the way insects guide themselves, in a manner which in its general characteristics approaches nearly to the truth.

As we have seen, the causes of the erroneous judgments with which Plateau has obscured the question at issue are errors of interpretation, inadmissible and continual generalisations, and the almost total omission of the psychical faculties of the insect, especially with regard to memory and association.

I cannot close this chapter without pointing out my full recognition of the defects resulting from the anthropomorphic nomenclature which I employ. But I prefer to treat this subject and to give my motives at the conclusion of these studies.

A FURTHER NOTE ON PLATEAU

In his most recent work (Vision in *Anthidium manicatum*, Ann. de la Soc. ent. de Belgique, xliii., 1899) Plateau states the following facts regarding this insect :—

(1) The male of *Anthidium* flies horizontally between the closely set stalks of the *Salvia horminum* without ever hitting itself against them.

Plateau now explains the fact by the movement of the insect. But he does not point out that this fact contradicts his old conclusions on analogous cases, especially with regard to the net, and even those of his experiments with the labyrinth, where the insect also moved, although more slowly.

(2) The said male hunts the other males of his species of the clump of *Salvia*. Therefore he sees and recognises them (from their movements, says Plateau !).

(3) Often it makes a mistake and throws itself on *Megachile*, *Anthophora*, *Apis mellifica*, even Ichneumons, to pair (naturally without success). Plateau concludes therefrom that its vision is bad, without noticing the contradiction to 2. But one knows that similar mistakes, due to excitement

of rutting, take place even among vertebrates. He notes further that *Anthidium* does not make the mistake with lepidoptera.

(4) Plateau observes that, at the time of the first blowing of the flowers of *Salvia horminum*, hymenoptera fly straight to those flowers situated on the sides of the stalk and never to the bunch of leaves or bracts, even more strongly coloured in pink or bright blue, on the top of the plant. He deduces therefrom that the colour does not attract them, but the smell. I deduce therefrom that they know how to distinguish by sight, and recognise a bunch of coloured leaves from the flowers which they are looking for.

CHAPTER X

ORIENTATION IN SPACE

A. *Sense of Movement* (*Senso-motility*)

MACH—BREUER

UNDER this heading I desire to treat in one mass a somewhat complex question which has given rise to peculiar opinions and to a curious mistake. Nevertheless let us say at the outset that there are two fundamentally different classes of facts to distinguish.

1. When we move in space, in common with other animals, we have the faculty of recognising our relative position and orienting ourselves. As far as we are concerned, we know that this is due partly to the combined sensations or perceptions of touch and sight which orient us, and partly to recollections. Thus, for example, entering into our bedroom on a dark night, we guide ourselves there rapidly, and put our hands on objects of which the place is known to us, not directly by the aid of sight or touch, but by means of *recollections* of the space of the said room, memories that our former visual perceptions have left us.

We do not possess any special sense of orientation; vision and touch, especially vision, and the memories of these two senses alone, or nearly alone, orient us in space and we are perfectly conscious thereof. Hearing gives little assistance, taste and the sense of smell practically none. That is the case in man, incontestably. The blind alone orient themselves by touch and hearing, for vision orients us more rapidly than touch and at a greater distance.

But we have already seen, whilst discussing Lubbock's, Plateau's, and our own experiments, that it is the same with insects as with the higher animals, though insects possess in addition a special faculty of orientation by means of the antennary "smell," a faculty to which we shall return. But the principle is the same. It is a sense, of which the disposition furnishes to the brain distinct relations between the different portions of space. Combined in the form of images, these relations are fixed in the brain, thus transformed into perceptions (*Wahrnehmungen*) and into recollections which are used in the orientation of the animal in movement.

I hope to prove that any other mystic or mysterious theory of special sense, sixth sense, magnetism, etc., is as superfluous as false for the whole animal series. The known senses, their varieties and the memories which are derived from them, explain everything.

2. It is especially to Mach [(1) Sitzber. Wiener Akademie, 6th November 1873; (2) Mach, E., *Grundlinien der Lehre von den Bewegungsempfindungen*, Leipzig, 1875; (3) *Ueber Orientirungsempfindungen*, Vortrag Wien, 1897, bei Braumüller] and to Breuer (Anzeige d. K.K. Gesellsch. der Aertze, No. 7, 14th November 1873, etc.) that we owe the solution of the question of the sensation of movement. There are therein several factors to distinguish.

(*a*) Every muscular contraction, every relative displacement, every pressure of one part of the body, stimulates tactile nerves, which thus acquaint the brain of the locality of the displacement. This is a question of a simple phenomenon of the sense of touch.

(*b*) We are conscious of the effort of every motor innervation. But Stricker and the muscle-reading of Cumberland prove that every effort of will, even if not followed by gross movement, is accompanied by an effective muscular innervation which can suffice to stimulate the sensory terminations. Thus (*b*) can be referred to (*a*), that is to say, to touch.

(*c*) Basing his conclusion on the law of inertia, Mach has, on the other hand, shown that we experience no sensation from continued movement as a whole, but that it is accelerations, retardations, changes of direction, undergone by the mass of our body, which excites sensation in us by the simple fact that every such change changes the pressure of parts of the body one on the other, and of the body on the objects which it touches and which uphold it. Here again the nerves of touch and sight (relative displacements of the retinal image) serve to acquaint us with the changes.

But Mach and Breuer have proved by ingenious experiments that we are conscious of accelerations, retardations, and rotation, independently of vision and touch. They have proved that the seat of this sensation is in the head, and that everything unites to localise it in the vestibulary apparatus of the labyrinth. The phenomena of sea-sickness, of earth-sickness (in the opposite sense), of rotatory vertigo, and of balancing are connected with this sensation.

Every acceleration of movement excites, according to its direction, some part of the terminal apparatus of the vestibule, the otoliths or the liquid of the semicircular canals remaining behind in virtue of their inertia, and thus shaking the nerve. The disposition of the three canals in the three dimensions of space serves to mark further the angles of change in the directions of the movement, *i.e.* the rotations total or partial in the three dimensions. Mach thinks that the vestibule itself serves to acquaint us with accelerations and retardations in the rectilinear progression of the body.[1]

I refer the reader to the original works of Mach and Breuer, from which it is clearly proved that the vestibulary apparatus orients our head and by it our body in all changes of position and of speed. Indeed, each movement is marked by a sensation of rotation or of progression which can become illusory when prolonged beyond a sudden stop, and which ceases when the contents of the vestibulary apparatus has itself taken the rapidity and direction of the body by the continuance of the movement in the same direction.

But various authors have exaggerated the bearing of the fact in thinking that they can extend it to orientation outside the body. The vestibular apparatus constitutes specially a sense of equilibrium, a static sense, in no way a sense of orientation in space outside ourselves. It is not even indispensable, since numerous deaf-mutes keep their equilibrium without it and only lose it under water, where the sense of touch of the body can no longer acquaint them with the variations of pressure. Mach calls the otoliths "statoliths."

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[1] Ives Delage (*Pourquoi les Canaux Demicirculaires sont disposés et conformés comme ils les sont*; Arch. de Zoologie, etc., 3me Serie, tome viii., 1900) has pointed out two important facts: (1) That, the semicircular canals being capillary tubes, their contained fluid can only act molecularly as a solid (a fact confirmed by the gelatinous matter replacing it in the large canals of the Elasmobranch fishes); and (2) That the canals of the two sides are so placed in relation with the cardinal planes of the body as to be co-operant one with another.—TRANS.

Mach considers that the organ of hearing (cochlea) is a phyletic specialisation of the vestibulary apparatus for tones. He thinks that in the lower animals hearing does not exist, but that the otoliths give the sensation of vibrations and that the organ of hearing is thence derived. This theory agrees with the hypothesis of Dugès, according to which the supposed hearing of insects is a false audition by perception of vibrations, an opinion to which I am so far an adherent.

To the objection of Hensen, who says there are animals without a labyrinth, therefore the labyrinth cannot be an organ of orientation, Mach ironically replies: Serpents have no legs and move along all the same; therefore our legs are not organs of locomotion! This irony would be very just if the objection of Hensen could be epitomised according to the syllogism above; but this is not the case.

It is necessary in the first place to prove that the equilibrium of an animal and the sensations of accelerations and the reverse are possible *without vestibular apparatus*, even in animals which possess one (deaf-mutes, etc.). Then it is necessary to prove, as we are about to do, that the recognition of our position in space is due to other senses alone, and in no way to the vestibular apparatus.

We have only, therefore, to admit that, in animals without labyrinth, its sensations are replaced by other senses. This is the more plausible since it is a question of relatively small animals, in which, as we have already pointed out, *the entire body* is often shaken by the least breath; hence, owing to the law of inertia, sensations due to differences of speed in the displacement of the different parts of the body are for the most part wanting to it. The least vibrations and their direction are communicated on the other hand to the entire body and to its organs of touch.

Finally the more we are able clearly to imagine at each instant, by the help of the visual memories, the localities of space and the objects which they contain, the less are we capable of imagining our muscular innervations and their play in the space occupied by our own body. This may be said also of all the more complex movements that we effect. We have certainly a vague notion of them, and our brain possesses an admirable unconscious memory of all the brain-sent innervations which govern them and of their co-ordination, without which pianists would be impossible, to give only one example. But we are absolutely incapable consciously to represent to ourselves the complex web of innervations called psycho-motor.

These facts being granted, have we the right to speak of a *sense* of accelerations or of equilibrium?

One ought to find at least one other word to designate the senso-motility and the unconscious memory that we have of the constitution of psycho-motor innervations. Precisely because it is unconscious in ourselves, we cannot study it there by introspection, and here "comparative psychology" is found on a level with human psychology, or somewhat near it.

Mach defends his sixth sense of accelerations by attributing thereto the sensation of rotation as the special display of energy of every stimulation of the nerve terminations of the semi-circular canals. This is a more palpable fact; but then it is necessary to distinguish this "*sense*" from the rest of the senso-motility as much as from external orientation.

In every case the vestibule, being entirely situated in the interior, cannot on this account make us acquainted with space outside of us.

CYON (*Supposed Sense of Space*)

By cutting through the semi-circular canals of pigeons, which are the termination of the nerve of the vestibule, the physiologist Flourens, as is known, regularly obtained a disequilibration of the pigeon's movements. The three canals are arranged in the three dimensions of space; the separate section of each canal produces a disequilibration and vertiginous movements in the direction of the said canal. These facts are absolutely certain and clear. I have observed them during several weeks on pigeons operated upon by Cyon. In the pigeons the canals are so removed from the brain, so large and so close to the surface of the cranium, that the objection of a possible cerebral lesion can only be made by persons who are ignorant of the facts.

Quite lately (Pflügers Archiv für die gesammte Physiologie, Bd. lxxix. Heft 5, p. 211, 1900, *Ohrlabyrinth, Raumsinn und Orientirung*) Cyon has resumed the subject and striven to establish his theory by new facts.

He has shown that a fish (Lampern; *Petromyzon fluviatilis*), which only possesses two semicircular canals, moves regularly and in a straight line only in the two directions corresponding to space forwards and upwards, never to the side.[1] But his experiment on the dancing mice of Japan are especially very interesting. This animal has only a single semicircular canal developed, the superior.[2] It does not move easily either

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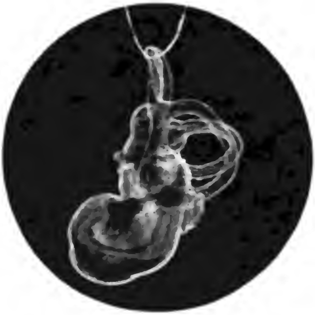
[1] If this statement is true, the Lampern would never be able to turn when it came to an obstacle. I have myself watched these fish, and have never been able to discern that they show any difficulty in swimming freely in all directions in their tank.—TRANS.

[2] I have left the account here given regarding the dancing mice untouched, although I do not believe it to be correct. It is certainly not in accordance with my own observations. The Japanese dancing mouse is a domesticated breed of the common house mouse (*Mus musculus*), and much has been written as to the condition of its labyrinth. Bonninghaus and Alexander (*Wiener klin. Wochenschrift*, 1902, No. 52) investigated the subject. The former thought that there was fusion of the canals, but Alexander could not corroborate this and claimed that he found some degenerative process in the nerves of the canals. Gray of Glasgow could find no difference whatever between the canals and those of the ordinary mouse, and, as I have seen and possess two of Gray's specimens (Plate ii.), I can confirm him. Moreover, I have had the opportunity of watching three typical dancing mice for several days and found that they were perfectly capable of executing any movement. They could turn with ease in any direction, were perfectly well able to climb an inclined plane of 45°, and could walk straight either backwards or forwards. The true secret of their "waltzing" appears to me rather to lie in the fact that the Japanese have trained them for very many years to waltz, *i.e.* to move rapidly in small circles, by keeping them in a very confined space. Rawitz (*Arch. f. Anat. und Phys.*, Phys. Abth., Leipzig, 1899, p. 236) states that dancing mice are also deaf, and owe their peculiarity to the fact that the outer and posterior canals are deformed and often fused, that the utricle is unrecognisable, and that the cochlear nerve is degenerated. Gray and I are of opinion that the wonderful discoveries which have been made in the labyrinth of these little rodents are due to the fact that they have been made upon microscopic sections, and that the deformities described are the result of the process of preparation. There is one very suspicious fact about Rawitz's figures. They show the horizontal (external) canal crossing over the posterior canal. This never occurs in mammals.—TRANS.

PLATE II.



Membraneous Labyrinth of a Japanese Dancing Mouse (*Mus Musculus var.*), from a preparation by Dr. Albert A. Gray

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forwards or upwards, but only by turning, diagonally. In order to go forward, it describes zigzag curves. Its perpetual amusement is to dance in furious and interminable waltzes, in which the male and female turn together; often even several mice dance together, without ever getting giddy, any more than deaf-mutes when they waltz. Between times they sleep or eat. They dance especially at night; it is especially the smell of their excrement which excites them to dance. They are almost deaf, only hearing the very high tone of their own voice. When the nose is stopped with collodion[1] they cease dancing. Every obstacle stops them. They cannot climb by day on a plane inclined at 45°. They cannot walk backwards, only obliquely. By night, when the height does not give them vertigo, they can climb on a plane inclined at 45°. It is not, therefore, any defect of locomotion that hinders them. Cyon concluded therefrom some connection between vision and the vestibule. Vision gives them vertigo, because they know the vertical dimension only by vision. A man placed on a height in darkness will probably feel giddy if the space is suddenly illuminated, as by lightning.

By the help of sight, pigeons with injured semicircular canals gradually learn to orient themselves, vision replacing the semicircular canals; but if they are blinded they lose their equilibrium again.

But, when dancing mice are blinded with collodion, they cease their normal movements and commence to turn somersaults in every direction, losing equilibrium like pigeons whose semicircular canals have been operated upon. They have to be put in a hammock to keep them from injuring themselves; the most they have learned at the end of several days is to make a few co-ordinated movements towards their food-box, and that in spite of the semi-circular canal which remains intact. They lose their faculty of dancing and make movements which they never make in the normal state. How can this singular fact be explained, when the same mice dance so well by night?

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[1] I did not attempt any of the collodion experiments described; it appears to me that any small animal thus blinded or with its nose stopped would make irregular movements in attempting to free itself from the unwonted discomfort. A cat with its head in a bag will throw back somersaults to get free.—Trans.

Cyon repeats on this subject his theory on the effect produced by the destruction of the semicircular canals in the pigeon.

He says that vertiginous movements arise—

1. From a visual vertigo produced by the contrast constituted by the semicircular canals now sectioned between space visible and ideal (ideally felt).

2. From the false representation of the position of the body in space, resulting from this fact.

3. From disturbances in the distribution of the innervation of the muscles, disturbances due to the same cause.

It is the third point only, that is to say the deprivation of the inhibitory influences on the innervation, which can explain how the dancing mice lose equilibrium after the occlusion of the eyes and not at night.

Cyon deduces from these facts that the replacement of the semicircular canals by the eyes is probably not due to conscious visual impressions, but to other stimuli, coming from the eyes, and which ordinarily are put in action by the semicircular canals. As early as 1877, Cyon considered the semicircular canals as regulating by inhibition the distribution and amount of the forces of motor innervation sent out to the body. Chevreul claims that it is their absence and not their presence that causes the disordered movements of vertigo discovered by Flourens.

Without entering into other details on the experiments made on sharks, etc., we will simply give the conclusions of Cyon.

(*a*) When one or other of the semicircular canals is congenitally absent, vision can partly replace its inhibitory influence, but only for the preservation of equilibrium in various positions of the body and for passage from one position to the other, not for orientation in space.

(*b*) The semicircular canals are the only peripheral organs of space. The sensations proceeding from them are indispensable to the representation of space (as regards the body itself).

(*c*) The faculty by which the animal moves in the different directions of space, *i.e.* orients itself, is obtained by the sensation of space of the vestibule. Sensations of sight and touch cannot replace this faculty.

The following is, word for word, the theory of Cyon on the "Sense of space."

A. Orientation properly speaking in the three dimensions of space, that is to say the choice of the direction in which movements ought to be innervated, and the co-ordination of the actions of the centres of innervation, necessary to the determination and preservation of the said direction, is exclusively the function of the semicircular canal apparatus.

B. The regulation of the forces of innervation, both for the said centres and for those which preside over the conservation of the equilibrium and over useful movements, is made principally with the aid of the labyrinth. But this regulation is at the same time made with the help of the sensory organs (eye, touch). These organs can more or less completely replace the labyrinth when it has been suppressed or when it is wanting.

C. The sensations produced by stimulation of the semicircular canals are the sensations of direction and of space. One is only conscious of them when the attention is directed to them. They serve for man to form the representation of space in three dimensions on which he projects his space vision and touch.

D. Animals which have only two canals are conscious of only two directions, and can only orient themselves in their domain. Those which have only one are conscious of only one direction (dancing mice), and only orient themselves by its aid.

Cyon presumed that the otoliths of the invertebrates played the same part; Yves Delage has verified this in Molluscs.[1]

Hensen has made to Cyon the same objection as to Mach.

The theory of Cyon is neither clear nor satisfactory. Positive and remarkable as the facts may be, the theory seems to me to attribute to the semicircular canals too general an influence. The matter does not appear to me yet cleared up, and we shall do well to accumulate new facts before forming the theory concerning it.

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[1] Also in some Crustacea. See this writer's paper, *Sur une fonction nouvelle des Otocystes comme organes d'orientation locomotrices*, Archiv de Zool., 2nd Series, tome v., 1887. For Coelenterates, see also Brooks, *The Sensory Clubs or Cordyli of Laodice*, Journ. of Morphology, x., 1895, p. 287; and Hurst, (1) *Supposed Auditory Organs*, Natural Science, vol. ii., 1893, p. 350; (2) *Suggestions as to the true functions of "Tentaculocysts," "Otocysts," and "Auditory Sacs," Ibid.*, p. 421.—TRANS.

I recall on this point my own experiments made on the auditory nerve of the rabbit (Neurologisches Centralblatt, 1885, Nos. 5 and 9; Archiv f. Psychiatrie, Bd. xviii. Heft 1, January 1887; then Onufrowicz Br., *Experim. Beitr. z. Kenntn. des centr. Urspr. des Nerv. acusticus.* Arch. f. Psychiatrie, 1885, Bd. xvi. Heft 3). In these works, made by me or under my direction, taking into consideration other facts relative to the cerebellum, I have obtained results that I think I can now sum up as follows:—

1. The movements produced by the destruction of the semicircular canals are repeated each time the nerve to the vestibule is injured in any part of its course up to its nucleus of origin, described by Bechterew as situated on each side, above the fourth ventricle, under the *vermiform process of the cerebellum.* This nucleus, composed of small polygonal cells, appears to have the character of a motor and not of a sensory nucleus. These little cells become in part atrophic, when one succeeds in establishing a partial but sufficient lesion to the nerve, without causing the death of the animal. Its total lesion produces perpetual rotatory movements until death; I have repeated the experiment more than once.

2. The cochlear or auditory nerve has quite another origin, similar to that of sensory nerves. The cells of its neurons are partly in the cochlea and partly in the acoustic ganglion I have described (Onufrowicz). Its lesion or total extirpation brings no perturbation of movements in its train, but subsequent atrophy of its centres of origin (acoustic ganglion, acoustic tubercle).

3. The extirpation of the cerebellar hemispheres of the rabbit do not occasion any perturbation of movements.

4. Even superficial lesions of the *Vermis* do not entail them; only deep lesions, which affect the region of the nuclei of the vestibular nerve, upset the equilibrium.

These results, we see, agree, as a whole, fairly with the theories of Mach and Cyon, and it appears to me relevant to quote them here[1]. B. v. Gudden and Schiff had moreover obtained the same results before me, so far as concerns the operations on the cerebellum.

Wlassak finally has removed the cerebellum of frogs without obtaining disorders of equilibrium.

But—and this specially interests us—insects do not appear to possess any organ of which the lesion produces analogous phenomena to those of lesion of the vestibular apparatus of the higher animals.[2] Lubbock interpreted as microscopic stethoscopes the flask-shaped and champagne-cork organs which Hicks and I have described in the antennæ of ants and bees; Graber has found supposed otoliths in the antennæ of flies, and has admirably described the sensory tympaniform apparatus of crickets and acrydians. Nevertheless all these organs can be extirpated without upsetting in the smallest degree the equilibrium of the insect. The halteres of diptera have, it is true, a sensory organ, and their section prevents flight; but they produce no other disordered movement (I have removed them repeatedly), and the prevention of flight has another mechanical cause. The only lesions which I have seen followed by convulsive and vertiginous movements in insects have been lesions of the brain (supraœsophageal ganglion) of one side alone or of other ganglia or ventral chains, a lesion which produces a circus movement; there are also the general convulsions which are produced by poisoning by morphine. One might, strictly speaking, add further, the spiral flight in the air of blinded insects (see above), but on earth these insects retained the perfect co-ordination of their movements.

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[1] Cyon thinks, nevertheless, he can prove that stimulation of the auditory nerve (cochlear nerve) excites the semicircular canals and gives a sensation of space. To that I reply that the extirpation of the cochlear nerve produces no movements of vertigo, and that sound gives us the worst possible appreciation of space. Think of a good ventriloquial entertainment and the manner in which the contrasts of the voice alone, which constitute the art of ventriloquy, are enough to put our judgment entirely at fault as to the direction whence the sounds proceed; then it will be clear how little the hearing alone teaches us as to space. I have seen a ventriloquist deceive, several times over, a pack of running hounds by imitating distant baying. He thus made the pack go off in whatever direction he pleased. The localisation of hallucinations of hearing made by alienists show also the arbitrary way in which we localise sounds in space. We localise them specially by evidence brought to our aid by the perceptions of other senses.

[2] I think that it is only right to refer here to my own experiments upon *Vespa vulgaris* (A Contribution to the Study of the Function of the Antennæ in Insects, *Proc. Zool. Soc. of Lond.*, 1905, vol. i. p. 85), in which my results are quite at variance with those of Forel in removing antennæ. Wishing to obtain some explanation of this discrepancy from one whose experience is so much greater than mine, I asked M. Forel if he could enlighten me. He replied, "Quant à vos guêpes, il faut que vous les ayiez trop blessées, car j'ai vu trop d'insectes voler et se diriger parfaitement bien sans antennes, même revenir manger du miel là où ils en avaient trouvé (abeilles). Essayez de *Vernir* la massue des antennes de vos guêpes au lieu de couper toute l'antenne."—TRANS.

But the lesion of the nervous centres seems simply to cause on the side injured a paralysis of the cerebral innervation (voluntary, corresponding to the pyramidal tract of vertebrates) which, augmenting the reflex activity of the injured side, necessarily gives a "circus" character to the movements, since they are inhibited by the will of the other side only. The three feet of the injured side therefore take command.

These experiments have, moreover, been performed in a systematic and admirable fashion by Alexander Yersin on the cricket (*Recherches sur les fonctions du système nerveux dans les animaux articulés*; Bull. de la Société Vaudois des Sciences Naturelles, vol. i. Nos. 39-41, 1857 or 1858), and I can only refer the reader to them. Yersin has constantly seen the insect turn to the side opposite to the lesion, whether of the supraœsophageal ganglion, or of one of the connecting cords situated below. He has shown the relative independence of the nerve centres among other things by the fact that, after section of a connection, the head of the cricket which wished to stop opposite a morsel of bread to eat it, or opposite the female, is thwarted by the feet, which continue to walk forward. If it holds itself there with its mandibles it turns a somersault. Apart from this he has been able to prove the existence of cross reflexes.

But of a "*sense of space*," according to Cyon's view, or only of equilibrium or of accelerations, we can find no trace. And, notwithstanding, does it seem that logic demands it? Either the theory is not exact, or, clearly, in insects the "sense of space," of equilibrium, and of the accelerations of the body is useless and does not exist, being simply replaced by the ordinary senso-motility by means of touch, etc. Is this perhaps because insects are deaf? I do not wish to go so far. I have simply wished to put the question on this point.

The same reflections and the same facts also serve further to place the theories of Loeb on a hypothetical, geotropic sense, presided over by the statoliths, into the limbo of the absurd. Even without such a sense, insects would not walk, any more than ourselves, on their backs or their head.

B. *Faculty of Orientation outside the Body and Supposed Sense of Direction*

Let us now pass to orientation for distance, such as takes place consciously in ourselves by means of sight and touch.

I will not repeat here what I have said as regards the way in which, according to my experiments, insects orient themselves, not only by the help of vision (especially in flight) and of the antennæ (especially on the ground), but by combining the perceptions of their different senses and the memories of their sensory perceptions.

I must emphasise that I always use the term *perception* in the sense of the German word *Wahrnehmung*, that is to say, of a complex psychical phenomenon of associated sensations, excited normally by actual sensory stimuli, combined with recollections of former associated sensations. A perception is therefore never primitive. Hallucination is an illusory perception, excited by internal stimuli alone, with the help of memories of sensory images.

I refer first to the remark which I made in 1886 on M. Fabre and the instinct of direction, and which is reported in the fifth chapter of this work (page 73). To this I add the following quotation:—

V.—A. Forel, "Revue de l'Hypnotisme, June 1893, p. 34, *Vision and Sense of Direction.*"

"Prof. Caustier (Revue de l'Hypnotisme, No. 1, p. 10, July 1892) is in too great haste to decide negatively the question of vision with the help of the rotundity of the earth. He forgets that pigeons, still more that *Chalicodoma* (insects more than 2 cm. long and resembling *Humble-bees*) store up in their brain visual images, memories of places travelled over during their independent excursions. Why do pigeons first raise themselves very high and turn the head in various directions? Why do they raise themselves above the mist before taking their direction? Why do a certain number of pigeons lose their way? Why does there exist a maximum distance (250 to 300 kilometres) beyond which pigeons usually appear no longer able to find their way? Why is it advantageous to repeat trial journeys in the same direction, increasing the distance little by little? Do not all these facts clearly speak for an orientation by vision? In dragging in the rotundity of the earth, one forgets its inequalities: the mountains. Mont Blanc is visible, from the plain, at more than 200 kilometres. But, in being raised on the wing to 300 metres, the visual field is considerably increased, less elevated mountains are seen farther off. But further, M. Caustier evidently starts from the idea (absolutely erroneous in my opinion) that the pigeon can only use its eyes to direct itself if, from the point where it is released, it directly *sees* the locality of its pigeon-loft. But I suppose that it is enough for it to recognise any landmark whatever situated between the two localities."

"But we can go further. The pigeon flies often and far. In its aerial excursions it goes a certain distance from its pigeon-loft. But, if it can recognise a landmark situated half-way between the place where it was released and the place (known to it) situated at the peripheral point of its ordinary excursions, in the direction of the place to which it has been carried, that is enough to guide it."

"These latter facts already diminish by more than half the distance which we must demand of direct vision. And what proof have we that pigeons do not instinctively use the sun and the other stars to guide themselves?"

"To these reflections we must add another incontestible fact that M. Caustier would also explain by the famous sense of orientation, it is that of the degeneration of the faculty of orientation in civilised man."

"This degeneration, already enormous when compared with the faculty of orientation of, for example, the American Indian, scarcely allows more comparison than our vision does to that, infinitely superior, of birds. The Indian has not only much more keen sight, but he knows infinitely better how to use it to orient himself. It is the effect of the exercise which we have lost, thanks to compasses, roads, railways, etc. In the bird not only is sight much more developed, but, as we have seen above, its position in the air and its rapid movements necessarily give it ideas of places of which we can only have a feeble notion. If a league for *Chalicodoma* (aerial) corresponds to 4 metres for the ant (terrestrial), 250 kilometres for the pigeon corresponds well to 4 kilometres for man, and the enigma is explained."

"Let us make, further, the following experiment. Let us obstruct by an ankyloblepharon, for example, the eyes of a pigeon, a cat, a dog even (here it is necessary, nevertheless, to take the sense of smell into account), and we shall see that the instinct of direction will have disappeared, and that these animals will be as incapable of finding their way, flying or on the ground, as the flies, humble-bees, and cockchafers whose eyes I had varnished and which started to bump themselves against the earth and against walls.[1] If the bees do not know how to find their displaced hive,[2] that is owing to their feeble reasoning, since sight always brings them straight to the old locality."

"We have therefore need of neither a sixth sense nor of electricity nor of atmospheric currents to explain to us the faculty of orientation in birds."

I confess that I feel a certain satisfaction in seeing the views which I expressed in 1886 and 1892 now entirely confirmed by Exner and by Cyon, as we shall see, without these two authors appearing to have been aware of my article.

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[1] As we shall see, Cyon made the experiment and obtained therefrom the result which I foresaw.

Romanes (*Nature*, 29th October 1886) carried a hive into a house close to the sea, situated several hundred metres aside, away from every hive, with flower gardens on each side, large lawns in front. He first opened the window and the hive to allow the bees to explore the immediate surroundings. Then, in the evening, he secured the bees which entered and put them in a box. Next day, leaving the hive closed, he carried the box to the edge of the sea, 250 metres at most from the hive, and released the bees. *Not a single one* found the way to the hive therefrom; none returned. He waited several days, to be certain that they were really lost, and thus repeated the experiment several times with the same result. But when afterwards he remade the experiment by carrying the bees to the end of the gardens at each side of the house, they were often found returning before him to the closed entrance of the hive in his room.

Romanes rightly concluded from this beautiful experiment that it is the knowledge of places and not a special sense of direction that guides bees. We have therefore arrived, he and I, at the same result independently of one another.

[2] Experiments made long before those of Bethe with the same result.

CYON AND TOUSSENEL

Viguier thought that carrier-pigeons were guided by terrestrial magnetism. Bonnier attributes to them a kind of automatic cartographic institute situated in the semicircular canals.

Cyon made experiments at Spa (Belgium). He noted the great development of the occiput and semicircular canals in carrier-pigeons; but he attributed, undoubtedly with truth, this development to their considerable muscular system and their enormous force of innervation for flight.

He first closed the eyelids of various pigeons with collodion. These animals no longer found their pigeon-loft at four paces.

Then he carried to a distance of 70 kilometres some pigeons in which he stopped the nose of one and the ears of another with collodion and a pledget of cocainised cotton-wool. He released them at the bottom of a dale.

The pigeon with closed ears returned to the house first, even before an intact pigeon.

The pigeon with closed nose only returned at the end of four days, after having lost its collodion.

In my opinion Cyon attributes too much importance to this last experiment, which is a single one and from which he concludes an orientation by the sense of smell. He should repeat it with more care. But he allows a predominant part to vision.

Cyon concedes to pigeons intellectual faculties and draws attention to the following facts:—

A pigeon carried from *a* to *b* by a detour *c*, *d*, *e*, generally returns by the same detour. But if, arrived at *d*, 100 kilometres from *a*, it succeeds, by describing several aerial circles, in recognising the direction where *a* lies, it flies there by the straight line *d*, *a*.

One often sees Belgian pigeons, released at Bordeaux, return by following the seaboard to orient themselves towards the north, instead of following the line of railway. Reynaud believed he could establish a "law of back-scent" in the orientation of pigeons for the return. These facts prove that this is a mistake.

When one is careful to take pigeons from the same pigeon-house, and, after having carried them a long way, to release them only at such intervals that none of them can see its predecessor, one sees that they all take at first somewhat different directions.

Cyon quotes, as do we, the education of pigeons by successive training; he deduces therefrom that they learn to know their way with their eyes and their memory, and thinks that they thus come to orient themselves up to 500 or 600 kilometres. Only he attributes to their nose a part in an orientation by wind, and believes that the known difficulty that they have in passing the Alps is due to the numerous cold winds of those mountains. The pigeon, says he, loves to fly against the wind, which brings it odours. Nevertheless he admits the possibility of a nasal sense (*Spūrsinn*) independent of the sense of smell. We prefer not to follow him in this hypothesis, which lacks sufficient foundation.

Let us notice again the opinion of Toussenel, an observer of great experience, quoted by Fabre in his Souvenirs Entomologiques (1882) (*l'Esprit des bêtes*).

"The bird of France," says he, "knows by experience that the cold comes from the north, the heat from the south, dryness from the east, dampness from the west. There is enough meteorological knowledge therein to supply it with the cardinal points to direct its flight. The pigeon transported from Brussels to Toulouse in a covered basket certainly has not the possibility of scanning with its eye the map of its journey; but it is impossible for anyone to prevent it from knowing, by the warm impressions of the atmosphere, that it is following the southern route. Restored to liberty at Toulouse, it knows already that the direction to follow to regain its pigeon-loft is that of the north. Therefore it pricks off straight in this direction, and only stops itself near the sky latitudes, the mean temperature of which is that of the zone which it inhabits. If it does not find its home at once, it is because it has turned too much to the right or left. In every case it needs only several hours of search in a direction from east to west to remedy its mistakes."

I was not aware of this opinion, which harmonises very well with my own. Fabre tries to refute it, but very feebly, with his cats and his *Chalicodoma*. There is no need to shuffle the cards. The sensory and mental combinations are other in the cat that does not fly. I certainly do not believe that the opinion of Toussenel explains everything; we have already found it wanting and we shall find it so again. But it includes an important factor of orientation, a factor which must be taken into account.

SIGMUND EXNER (*Negative Versuchsergebnisse über das Orientirungsvermögen der Brieftauben.* Wiener Akad. d. Wissensch. Mat. Naturw., Cl., July 1893)

Even before Cyon, Exner had made experiments of another kind as follows:—

The pigeon loves his pigeon-loft above everything, and knows how to return to it from great distances. It is this instinct which is utilised. It is certain even that, of the pigeons carried from the United States to London, three were able to return across the ocean.

According to the theory of Mach-Breuer, the otoliths constitute an apparatus serving to perceive the rectilinear accelerations which the animal undergoes in any direction, and the semicircular canals constitute an apparatus serving to perceive the accelerations which affect the animal whenever it turns round on any axis whatsoever. Exner has sought to explain the faculty of orientation of pigeons thereby. He has made experiments, and he admits that they have compelled him to abandon his hypothesis. They are these:—

He carried his pigeons in a basket (closed by a black cloth), which he shook all the way or which he made to turn on its axis with great rapidity. He did this from the departure to the arrival in the station, on the railway, at all the turnings. Three pigeons were put into the basket, shaken and turned. The other three were neither shaken nor turned. He transported them to 37.7 kilometres from Vienna, to a place where the said pigeons had never been, according to the opinion of their owner, and separated from Vienna by the mountains of the Wiener Wald.

The pigeons were released one after another, not one before his predecessor had disappeared. All returned normally to the pigeon-loft. The (unshaken) control pigeons were released first.

Here I must be allowed to observe that the experiment is insufficient. The fact that our eyes no longer discern a pigeon does not prove that the pigeons no longer see it. Then he ought to have released the shaken ones first. In every case shakings and rotations did not in any way disorient them.

In the second experiment, Exner not only kept his pigeons turning all the way, but galvanised their heads with an electric current by a very ingenious proceeding.

He thus galvanised two pigeons, one old and one young, and took with them two control pigeons, one old and one young. He carried them all four to 54 kilometres from Vienna, under analogous conditions to the others. The old galvanised pigeon returned to Vienna to his pigeon-loft in 3 hours 32 minutes. The old control pigeon only returned two days after. The two young pigeons did not return, neither the control one nor the galvanised one. The latter remained at the place of departure. This experiment is absolutely conclusive, the pigeon which was turned and galvanised arriving first.

Let us note that it was the young ones, those which had as yet seen little of the country, which were unable to find their way! These pigeons had been equipped with a mask of black cloth to prevent them from seeing. A control experiment with unmasked pigeons gave three pigeons lost out of four! It is therefore the chain of mountains and the unknown place which disoriented them!

Finally Exner made the experiment again at 28.8 kilometres' distance and without the mountain range between the two, but letting the galvanised pigeon and the others rest during two days in the different places before releasing them.

The result was that the galvanised pigeon returned second (in 40 minutes). In spite of all, Exner holds to a static sense. We will not return to this, but refer to what we have said as regards Mach, Cyon, and the insects.

Then Exner put himself the following question: Do the pigeons acquire knowledge on their journey out?

He therefore narcotised two pigeons during the whole journey of 43 kilometres and left them four days at Oberhollabrunn, separated from Vienna by a hilly country. Then he released them, also a control pigeon. Two were lost, including the control pigeon. Only one of the narcotised birds returned in 4 hours 20 minutes.

He made the experiment again at a less distance with two old and two young pigeons, of which one of the old and one of the young were narcotised. *The two young ones were lost. The two old ones returned, the narcotised in less time than the normal one.*

I am astonished that Exner does not draw from such clear results the simple conclusion that it is the experience and the knowledge of places by vision that orients pigeons.

In conclusion, I myself suggest a very simple experiment to the pigeon-fanciers, as follows:—

Hatch several carrier-pigeons' eggs in a big cage placed in a chamber, the window of which shall be simply obstructed by a frame of muslin or other stuff, thick enough for a view through it to be impossible, even for a pigeon. The air could penetrate sufficiently through the muslin, as well as diffuse light. When the young pigeons can leave their mother, take her away. Then the young pigeons will be allowed to grow up in their cage, without ever letting them see anything of the country through the window. Once they shall have the strength and age required, let them be carried, the head covered by black cloth, in a well-shut basket, not to 20 or 30 kilometres, but only to *2 or 3 kilometres'* distance, after having removed the muslin from the window. If they find their pigeon-house by the help of a magnetic, static, geotropic, or otolithic sense of space and direction, I will surrender to the evidence and declare myself beaten. But if they do not find it, I have the right to deny absolutely the existence of the said supposed sense and to attribute orientation to vision.

Nevertheless, two precautions are still necessary; it is necessary that the window of the chamber, where the cage or pigeon-house of the pigeons will be, be placed in such a manner that the contents of the said room cannot be seen directly from a distance. It is further necessary to isolate the mother from the young pigeons, so that she cannot serve them as a guide.

I am persuaded that the pigeons would be absolutely incapable of finding the way to their pigeon-house, even at this short distance, for the simple reason that they will have no visual recollections outside of the room where they will have lived.

Exner has, by his last experiment, refuted the idea of knowledge acquired on the outward journey by the pigeon, but in no way the facts of their antecedent knowledge of the places. But it is upon this that I insist.

FABRE (*Souvenirs Entomologiques*, 1879 and 1882)

Let us return to insects and to M. Fabre. Perhaps it will be thought idle that I should have talked so much pigeon apropos of insects. But this was absolutely necessary, for one is completely led away in this question. I consider I have shown that the way in which birds orient themselves is the same as that in which aerial insects do so, and that in a striking manner. From that to conclude that the semicircular canals and otoliths which are wanting[1] in these latter are probably of no account is only a step (compare with Yersin's experiments and mine, see above). Then a large concourse of facts agrees in proclaiming vision as the aerial sense of orientation *par excellence*, the sense which makes every hypothesis of a mysterious sense of direction useless. The only restriction to make is that the sense of smell, touch, and hearing serve it as a complement, more or less important, or even surpassing it among certain animals (Bombycides, bats, and others).

In the experiment of Fabre of which we have spoken, it is necessary to mark certain details. The *Chalicodoma* (mason-bees), marked with colour, which he carried in a box to 3 or 4 kilometres, only returned most of the time in a proportion of thirty to forty per cent. Of the forty *Chalicodoma* which he carried into a wood 5 kilometres from their nest, nine only found their way back. Without doubt, as Fabre says, the pressure of his fingers crippled some; but *Chalicodoma* are very hardy, and this fact is in no way enough in my opinion to explain the number of lost ones. In most of the cases the *Chalicodoma*, after rising in the air, went straight off in the direction of their nest. There were, nevertheless, a certain number of exceptions; some took another direction.

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[1] What Graber believes to be an otolith in the antennæ of flies can be removed without the equilibrium being disturbed the least in the world. The organ of senso-motility in insects, if it exists, is yet to be found.

In the experiment at 5 kilometres' distance, the wood was separated from the nest by a little hill 100 metres high. Freed in a glade, the *Chalicodoma* at once soared and described several circles (like pigeons), then all went off towards the south, in the direction of the hill, which was that of their nest. Why did only nine return? If a mysterious sense of direction had guided them, all that started would have returned. Weismann thinks rightly that the bees, set free in this unknown and, to them, distasteful place, would have been attracted by the sight of the hill. Once there, the oldest, those which knew the surroundings best, would have found a landmark and their road. Indeed we see even pigeons often go off in various directions at first.

Instigated by Charles Darwin, Fabre did with his *Chalicodoma* the same experiment as Exner with his pigeons. He shook the box which contained them and made it twist about to disorient the *Chalicodoma*, taking care, further, to go by various devious roads. The effect of the twisting about was absolutely *nil*. The *Chalicodoma* returned in as large numbers as without twisting.

Charles Darwin having then given Fabre the suggestion of terrestrial magnetism, Fabre tried to disorient his *Chalicodoma* by putting on their back a little magnetic needle. But these insects suffer neither needle nor straw on their back in flying, which made the experiment fail.

Is it not significant thus to see mason-bees, placed under the same experiments, conduct themselves in miniature almost exactly like carrier-pigeons, without possessing, however, any vestibular or otolithic apparatus? The circle of their knowledge of places does not appear to go beyond 4 kilometres; that of highly trained pigeons appears to reach to 500. There is no striking disproportion therein.

ALBRECHT BETHE[1]

Bethe starts with a preconceived idea. For him insects are reflex machines, and all comparative psychology is an absurdity. He holds all his predecessors cheap; according to him they are evidently very feeble. We shall have to return to this subject later. Here we have only to examine his experiments on the orientation of bees and ants. I only think it is necessary first to point out the fact, because systems and prejudices always influence the experiment. I further think that the extreme opinion of Bethe will have the good effect of making the questions precise. To be mathematically exact throughout, Bethe no longer speaks of vision nor of the sense of smell, but only of photoreflex, chemoreflex, matter of the nest (instead of the smell of the nest), etc.

A. BEES.—Bethe first asks himself if it is an odorous substance (a chemoreflex; I shall here allow myself to retain the old terms, having good reasons for not adopting the terminology of Bethe) which brings the bees to their hive. He declares that the hive has an odour which we perceive, and points out the males of Bombyx which, attracted from a distance by the smell, go to find their female in a town. He supposes that if one could prove it, that would suffice to make the hypothesis of mental faculties in the bee superfluous. Let us point out that this reasoning is too artless, for bees do other things besides returning to their hive.

Bethe changed a hive (A) in place, but only for one breadth of hive, and put in its old place an empty hive (B), therefore quite beside it. The bees returning from foraging flew straight to the door of the hive B (which occupied the old place of their hive A). They entered the empty hive, finding nothing there, left it by the back, then flew afresh to the entrance, thus making a perpetual circle.

The bees of the hive A only went out hesitating, little by little; some flew away; they were upset by the novelty (odorous) of the departure platform. But at the end of ten minutes a good number were gone. At this moment the first bee went again to the entrance of A, but instead of entering by the door of the hive, it ran over the platform buzzing its wings, which the others imitated. None entered the hive; some flew to the door of B. At the end of twenty minutes about $\frac{1}{20}$th of the bees flew to A, the remainder to B. Finally one of the bees which wandered into the empty hive B discovered, in ferreting about on the prowl, an interstice which led to the hive A. Others followed it walking, and thus formed a file from the hive B to the hive A.

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[1] Albrecht Bethe, *Dürfen wir den Ameisen und Bienen psychische Qualitäten zuschreiben?* Archiv f. die ges. Physiologie, Bd. 70, 1898.

Bethe concludes *with certainty* that chemical traces served to guide the bees, walking at least, and that even on the wing a chemical substance also helped to guide them, since several new arrivals flew to A *because* the bees which had left A had left their odour (chemical trace) on the departure platform (*Flugbrett*).

I do not admit these conclusions for reasons given above and proving the bad sense of smell of bees (Plateau). First the bees could follow their companions walking by sight as well as by smell (they do it with cut antennæ), which is enough to refute the "certainty" of Bethe. And further, the bees flying straight to A were without doubt those which had left it and found the direction by vision or saw other bees there; here one can even certify it from our experiments (Plateau) which Bethe mistakes.

But Bethe himself recognises the absurdity of the hypothesis of an odorous trace in the air, a trace or scent which every breath would sweep away.

Our author turned a hive on its axis 90°. The bees which returned flew to the place where the door of the exit used to be, alighted on the hive and buzzed their wings (Bethe calls this buzzing of disquiet "*heulen*"; let us also call it "crying," for short). At first they did not know how to find the displaced door of entry and only found it walking, even when the others were flying out.

Our author placed his hive on a pivot which he could turn horizontally, with the desired slowness, and made it turn at the rate of 90° in a quarter of an hour from east to south. At 30° the bees still went fairly straight to the door, without stopping. But at 45°, at the end of seven minutes, the greater part of the bees arriving began to flutter several times before entering, which caused a swarm to accumulate; nevertheless the whole deviated towards the south. According as the rotation advanced, the swarm grew, and an increasing number of bees ceased to find the way at the gate of entry. At 90° the swarm was considerable; a few bees only succeeded in finding the door. Several alighted on the hive and discovered the door on foot. The greater number flew in swarm in the intermediate direction of 45°. If the rotation is slower (twenty minutes for 90°) the swarm follows the movement a little better (well up to 45°), but at 135° scarcely any bee found the door. A still slower movement gave no further result. Bethe could not make the swarm of bees arriving deviate to more than 45°. When Bethe left the hive turned for four or five hours to 45°, then replaced it suddenly in its normal position, the bees which had become used to flying to 45° (south-east) continued a certain time to fly in this direction, making at the last instant a turn to the right to enter the door. This flight to the south-east and this twist did not occur if he replaced the hive immediately after the seven or ten minutes of rotation.

But here is something better. Bethe put back his hive 50 cm. Then the bees flew to the place where the door had been, then described circles in the air. In doing this they passed right in front of their hive, and part of them entered it. Nevertheless a certain swarm was formed where the door had previously been. If he withdrew the hive *two metres*, scarcely any bee found the door. An enormous swarm formed in the air exactly at the place where the door was previously, that is to say, two metres in front of the hive. At the most, one bee found the actual door of the hive every two or three minutes. All the rest flew in circles of 0.20 to 2.5 metres round the old spot in the air. If the hive was replaced in the old spot, the whole swarm precipitated themselves on it. If one put in its place an empty case provided with a hole in the spot where the door of the hive had previously been, the bees flew to it and entered it in a more or less hesitating manner. It is even a trick known to bee-keepers to make bees enter a new hive.

When the hive was displaced forwards, instead of backwards, the result depended on the line that the bees followed (at the time when it was done) to enter their home. If this line was nearly horizontal, the hive could be advanced more than a metre without hindering the bees from entering. But if it was abrupt (descending rapidly), so that a displacement forward of one or two metres made it fall behind the hive, the bees arriving missed it, and began to form a swarm in the air behind it at the old spot of the door, as they did in front in the preceding experiment. It may be said in passing that this is a pretty proof of the influence of the purpose and obsession of the bee on the homeward journey.

If the displacement of the hive took place slowly and gradually, it made no change in the final result. The swarm, at the spot where the old door was, formed just the same in front or behind. At the most the number of bees which found the door was a little greater.

Bethe adds again that the bees whose antennæ he cut off flew in spite of it in a straight line to their hive from 25 to 50 metres' distance (same result as my own).

From these experiments Bethe concludes that the *Neststoff* (sense of smell) cannot play a preponderating part in the method by which flying bees find their hive. Something independent of the hive guides them. This something does not lead them to the hive, but to the place in space at which the hive is usually found. The sound or cry of the bees (that is to say hearing) does not guide them, otherwise their swarm ought to follow the displaced hive where their companions cry.

We will return to these conclusions. But Bethe considers he proves that it is not visual memories which guide the bees. The following are his experiments in this respect :—

A hive was exposed to the east and the bees flew to the east in leaving and in re-entering. Bethe turned the hive on several days towards the south (90°). For several months after the bees always flew to the east. The hive was surrounded by plane trees 6 m. high, those on the east and the south at 6 metres' distance. To the north-east and to the east were two free spaces; the bees flew by that on the east. Thinking that the light of this space was perhaps the cause of the phenomenon, Bethe placed a large dark-brown screen, 3 m. broad and 2½ m. high, so as to obstruct the said space. The bees were not worried by it, flying over the screen, and going one metre above the screen; the returning bees did the same. Bethe thought that he could conclude that they only saw the screen at 1½ metres' distance and that they had an instinct to fly east. In my opinion the fact does not permit of any such conclusion, there are too many other possible factors, especially the more ordinary; the bees liked to forage on the east side, and followed by mechanical habit their old direction almost close to the screen.

Bethe remade the experiment of Fabre with the rotations and even (with success) with the magnetised needle suggested by Darwin. Neither rotations nor magnet placed on the back prevented them from finding the way. This was to be expected.

Bethe has remade our experiments by varnishing the eyes of bees, and has observed the same flight straight into the air and the impossibility of orientation. But he quickly rid himself of this fact by declaring that light is the stimulating agent which excites to flight these diurnal animals and which "*directs them.*" Therefore the fact that the blind no longer know how to find their way "proves nothing" according to him.

I must protest against this allegation, as risky as it is arbitrary. It rests upon a false observation. Plateau and myself have shown that *Eristalis*, *cockchafers*, *nocturnal* and other insects *fly spontaneously with their eyes varnished.* But they are then incapable of directing their flight. This simple fact reduces the allegations and argument of Bethe to nothing. Nevertheless what is "*to direct*" the flight, if not to orient it? These are words and nothing else.

Then what did Bethe do? He hid a hive placed on a table two metres from a plane tree. The bees flew east-north-east. Bethe placed at 1 m. 50 from the hive to the west and to the south a corner folding screen 2 m. 50 high, with wings 2 m. 5 broad. He placed some coloured handkerchiefs on the screen.

Then he covered the table and the hive with green branches and glued blue paper on the yellow anterior face of the hive. The bees returning to the hive only hesitated a moment, forming a slight swarm. Then they flew from that time, without hesitating, to the door of the hive. Next Bethe placed 6 metre squares of white paper on the turf, in front of the hive. Then the bees became unquiet and flew hesitating over the hive. Bethe replaced the white paper by blue, and they were quieted. He explains the matter by saying that the bees shunned the large white surfaces lit up by the sun.

All that proves nothing at all, or rather shows we are right against Bethe. It is not exact that the bees shun the white. I have seen them foraging in a mass on white paper in the full sun, as well as on blue. And the bees of my hidden dahlias knew well how to find the locality without hesitation. The fact of covering our house with trees and placing a screen behind would no more hinder us from finding it, if it was not carried elsewhere. One must know the psychology and the adaptation of the bee to the entry of his hive, which is everything to it, very badly to expect any other result. The subjectivism of Bethe shows itself in the following fact. After having "quieted" his bees by replacing the white paper by the blue, he agitated them afresh by replacing the blue by a red one. He firmly believed in their inclination for the blue and their disgust for red and white. I note the fact without returning to it, for Plateau and I have shown to satiety that the question is one of an illusion.

Bethe recognised that in various cases (mirror reflecting the sun, fresh paper put round the hive, red paper, white paper) the bees are embarrassed and accumulate in a swarm before entering. But he explains it all by the sense of smell, and holds that the changes of aspect of the entrance of the hive do not prevent the bees from finding it without hesitation. With these restrictions I do not doubt this at all. It was to be foreseen, but it does not prove what Bethe wishes to prove. On the contrary it proves that a great and startling change of colour succeeds in disorienting them, even for the locality of the entrance of their hive, which is what they know best.

Some hives situated to the east were shaded by a plane tree of seven metres, situated right in front. Bethe threw it down on June 14th, 1897, at 10.30 A.M. Most of the bees were away foraging. As a matter of fact they re-entered straight through the door of the hive, without hesitating, across the open space where the plane tree was an instant before, whilst formerly they flew high, to pass over the plane tree.

The fact is doubtless interesting. But, the plane tree being no longer there and the hive not having changed its locality, it is not so extraordinary. Bethe thinks he has victoriously refuted thereby the memory of places in the bee. I deny it. The fact of the sudden disappearance of a big tree which hid a hut to which we know the road in no way hinders us from going straight to the hut—quite the contrary. Only Bethe thought he was able to conclude, from his experiments with the hive moved backwards, that the bees did *not see* the displaced hive, and this false conclusion leads him to others. They see it very well, but they are *preoccupied* with something else: their attention is obsessed by the recollection of the place where it was previously, and it is there that they obstinately seek for it. Similarly the bees perceived without any doubt the disappearance of the plane tree. But this plane tree was absolutely indifferent to them: at the most it inconvenienced them. Their attention took them violently to their hive only, which was not displaced, but straight in front of them. In denying the psychology of insects, Bethe naturally neglects to take it into account. A man would doubtless be stopped and would have reflected on the unexpected change. But a bee is not a man and reasons much more simply. It has no time to lose, and only associates that which is directly connected with its requirements and its instincts, which was not the case with M. Bethe's plane tree, as concerns the return to the hive.

Bethe then took up the experiment of Romanes, quoted above in a footnote, in another way. On one side of his garden is the town of Strasburg, where bees never go, so to speak; on the other are the fortifications, with meadows covered with flowers and bees. Bethe took marked bees and carried them on repeated occasions either to the town or into the vicinities of the fortifications, 350, 400, and 650 metres from the hive. They returned as well from the town as from the meadows.

The bees thus released first flew spirally upwards, then went off in a straight line in the direction of the hive, says Bethe. Of six bees released in a street lined with high houses, four flew in the right direction, one in a wrong one, one was doubtful. Eight others all flew in the right direction, etc. Bethe supposes that they took this right direction before having reached the tops of the houses, therefore before having been able to orient themselves by vision. I acknowledge that this last fact has perplexed me, for it has a conclusive aspect. Nevertheless, on reflecting upon it, and as I know Strasburg with its narrow streets, I have put myself two questions, as follows. How can bees take, in a narrow Strasburg street, the exact direction of their hive situated at the periphery of the town, before having reached the roofs of the houses? A street has only two directions. Did Bethe choose streets straight and just at right angles to the line of his hive? He does not say. Then he has not proved to me that the bees do not visit a town like Strasburg, where there are enough flowers, trees, sugar, and honey to attract them. In every case there are contradictory results there which require confirmation. In my opinion the experiment of Romanes is much more conclusive and better made than that of Bethe, because it left no other interpretation possible, because of the precautions taken. The hive of Romanes was newly brought to his garden.

Bethe finally grants something to vision. He shows that a piece of squared black paper is taken by the bees for the entrance door of their nest, and that they fly to it, whilst they are turned aside by white or coloured paper.

Bethe admits three kilometres in round numbers as the distance to which on an average bees find their hive. According to his idea, it is the mysterious force which acts up to this distance from the hive.

He decrees and concludes from his experiments that a *totally unknown force*, and not sight, nor smell, nor magnetism, leads them to the hive.

He quotes, further, several interesting facts: when he moved a hive back only 20 to 30 cm. each day, and let it remain during one day when a small swarm formed in front, he was able to succeed in retiring it to four metres without the bees returning to the old place of their door of entrance and exit.

When a hive was displaced in autumn, and put somewhere in the neighbourhood (three kilometres, in round numbers), the following spring the bees did not return to the old place, but to the new from the very first. (What then became of the mysterious and unknown force? Ought Bethe not to conclude from it rather that during their winter sleep they had forgotten their old aerial routes and were oriented afresh?)

If a hive is made to turn on its axis 90° during the night, and if several days of rain follow, at the first sunny day an obstructing swarm is formed of returning bees. But they soon find their way, and at the end of a few days they fly straight to their door. (Is it not a proof that the memory of the direction which they previously followed, and consequently the corresponding obsession, has lost its force during their seclusion [Forel]?)

The same result is obtained on sunny days if the hive is only turned several degrees day by day, Bethe having turned the hive thus slowly from east to south, left it for five weeks, then suddenly replaced it to the east. The bees returning from foraging then flew to the south, forming a slight swarm of hesitation, but soon they returned by a cast to their door, to the east. The swarm of hesitation quickly ended, but the bees continued to fly towards the south and to enter their door by making a cast; the cast was continued for weeks, but diminished in size little by little.

This charming observation is explained in our opinion by a phenomenon of fixed habit, but corrected each time by a moment of attention. We observe phenomena bordering thereon in ourselves. The habit of flying towards the south had lasted only five weeks. It had been preceded by a "habit to the east," and it is because of this that a little attention caused by the disappearance of the doorless wall was sufficient to make the bees go back by a cast to their previous custom, not yet forgotten, instead of throwing them into a complete disorientation as in the experiments quoted above. There is in this a luminous trace of insect psychology which recalls especially that of our subconscious conditions, of our somnambulistic automatisms for example.

But Bethe has made, further, other curious observations, which at first sight seem to make him right. We have seen above the story of the felled plane tree. Well, for months, whilst the bees returning to the hive flew straight to the door, those which left continued on the contrary, without rhyme or reason, like automatons, to fly upwards and to turn around the place in the air which was formerly occupied by the plane tree. Bethe sings of victory and thinks he has freshly refuted the habit and proved the mysterious force of return to the door. Let us analyse the facts.

The bee which has finished pillaging has only one fixed idea in its head: to return as quickly as possible to the door of the hive. This idea impels it to shorten every angle, to find the straightest line (the famous *Bee-line*) to reach its single objective. The case of those setting out is quite otherwise. Doubtless there is generally a principal direction by which they go out, that which takes them to the places where they forage. But in flat country these places vary according to the seasons, and with them the direction that the bees take in leaving their hive. I can affirm this, for we see it here. A field of colza in flower, situated to the north-west, makes them fly north-west, etc.

The bee which sets out is going, further, to forage in divers places. It has not, therefore, any fixed idea which impels it towards a single point at its start out. Hence an old automatic habit of flying in the air can be retained for want of any antagonistic idea.

Bethe is also astonished that the bees of a new hive, brought far and placed at his house, after elevating themselves, turning and setting out towards the south, returned later by the east. He again saw in it his mysterious force; I only see in it their excellent faculty of orienting themselves in space by vision.

Finally, Bethe carried some bees to a distance away in boxes, to see if they knew how to return to the hive. Those which were no longer capable of guiding themselves, after elevating themselves and having turned at a great height, always came to fall again exactly at the spot from which they had set out, without being more than several centimetres wrong. The bees set off from a box which he held in his hand; he altered his position after their departure. The bees returned to turn in the air exactly at the place where Bethe had previously held his box (in other cases on the meadow exactly at the place where the box had been from which they had started).

These facts are doubtless very curious, and prove without any doubt that there is in bees a surprising faculty of finding any point whatsoever in space. In the last cases the bees, being absolutely lost and unable to recognise the way to their very distant hive, had only one single recollection associable with localised space, that of the point where they had been released. There is therefore nothing astonishing in such a case in that they should, after having vainly sought to orient themselves in the air, return there, and there repeat the evolution which they make at the door of a displaced hive.

What is striking, in this case as in others, is the rapidity and sureness of their orientation in space. The objects in themselves, if they have not special attractive qualities, attract the bees much less than the circumscribed place of space which they know and recognise. This also proceeds, moreover, from the experiments that I have described in regard to Plateau.

Is there a sufficient reason, after all we have seen, to attribute to them a mysterious force independent of the senses and especially of sight? I do not think so. I do not wish to repeat what I have said regarding pigeons, but still to insist on a single point: we men, with our gentle terrestrial movements, are unable to understand (to feel, to imagine) what the orientation by vision of an aerial animal in rapid flight must be, with its innumerable and prompt displacements in space. Bethe, and many others with him, forget that to assess what a sense can do it is necessary, not only to take account of the number of its elements and of its acuity, but also of the way in which the animal can utilise it. A sight which bounds in the air, as that of aerial insects, must necessarily furnish its possessor, by hereditary adaptation from selection and with the help of rapid associations, an admirable faculty of orientation in space, since this became useful, as is the case with the social hymenoptera. What is not sufficient to orient us, suffices to orient a bee by vision, since its instinct, its percipient ideas impel it thither.

We have seen (Exner) that the faceted eye furnishes a superior perception of displacements to ours. But, in orientation on the wing, everything is displacement or relative movement. Without doubt the vision of bees and insects generally is not our vision. I plainly grant it to Bethe, and I have not ceased to prove it in a hundred ways; it is very much worse for certain things, but better for others. But Bethe, who is of an exaggerated severity for everything which savours in the least of anthropomorphism, even for the most permissible studies by means of analogy, himself falls into the narrowest anthropomorphism in putting his dilemma, which is nearly this:—

"Bees do not orient themselves *like man* by vision. Therefore it is not by sight, but by a mysterious force that they orient themselves." This is at least the sense of his one-sided logic. For him there is no possible middle course. For us quite the contrary. We say *Natura non fecit saltum.* Vision, like the sense of smell, is modified and adapted to the most varied ends. Further, the way in which the brain uses it varies with the aptitudes and the tendencies of this latter. Thence so many shades, so many variations, so many complications. If Bethe worked on his wasps, he would see at once how differently this social hymenopter, a connection nevertheless of the bee, orients itself, thanks to a much more developed sense of smell and to a different sight.

Bethe concludes at the end of his account: "Bees obey a force which is absolutely unknown to us and which forces them to return to the place in space from whence they came. This place is usually, but not necessarily, the hive. The action of this force only extends to several kilometres in round numbers."

We are very much indebted to Bethe for his ingenious and patient experiments. They enrich our knowledge by very interesting facts.

But I am obliged to combat his conclusions as preconceived, one-sided, and of an absolutism quite contrary to logic and to the scientific spirit.

In passing, I have made a series of objections of detail to Bethe's experiments. He himself is obliged to grant to the rest of his own experiments that he produced in bees a kind of habit (impulse), and that they were also broken of them. But what is a habit without memories? Do not Bethe's experiments speak clearly against him? At the end of five weeks bees still have the recollection of the old position of their door, which had been altered. But in the spring, after the winter sleep, all is forgotten.

Why did one party of bees released five kilometres away recognise their way and the other not? The unknown, blind force of Bethe, which led them to the hive, ought to be the same for all. And why did they first raise themselves in the air, wheeling like pigeons, to reconnoitre? The blind force could draw some more quickly, others more slowly towards the hive, and others to the place at which they had been released. On the contrary, the difference is explained simply if it is admitted that some had found landmarks which oriented them, others not. These latter, doubtless the youngest, as with pigeons, had not then any resource but to turn on their tracks, like every animal or man that is lost.

And finally, I again insist that if a force independent of vision guides insects in flight, insects with varnished eyes would orient themselves exactly, after having flown off: the objection of Bethe, indicated above, is no objection, it is a misstatement.

But other considerations show again the error of Bethe's position. I have spoken above of a nest of humble-bees (*Bombus*) placed on my window, and of the enormous trouble that the insects had to find it again, as well as of the way in which they first examined other similar windows before finding it. The humble-bees have less power of localisation than hive-bees; I think I have the right to affirm this. In every case this experiment speaks absolutely against the "unknown force" of Bethe. Such a force ought to have brought the humble-bees in a straight line to their nest.

To obtain an exact understanding of the orientation of insects in flight, it would be necessary for us to be able to think like them. The problem is doubtless made much more difficult by the fact that we cannot do so. But that is not a reason for throwing the handle after the hatchet, as Bethe did, and renouncing all analogies. If there are fallacious analogies, there are on the contrary very suggestive ones. The key of the matter by which we may approach the truth is to distinguish them as much as possible.

In our own case, to see, to look at, and to understand are three processes, but we only see well what we look at and especially what we understand. We are blind (in spirit) for things we do not understand and for those which do not attract our attention. We often pass things on one side, as if we do not see them. But everything goes to show that it is the same in insects. Only as 99 out of 100 of their acts are produced in a way automatically fixed by heredity, it necessarily follows therefrom that they only understand in their small and limited fashion the 1 in 100, perhaps, of what they do. That is why, dazzled by this immense automatism of instinct, we are forced to reason like Bethe, to see instinct only, and to be astounded, like Fabre, before the stupidity of this insect which is disoriented by cutting the thread of its acts, and which only knows how to search for the orifice of its destroyed nest; not seeing its larvæ, upon which it walks; or of those bees which buzz for hours in the air two metres in front of their hive, without understanding where it is, and what it is that is before them.

But, as I have said, man in somnambulism offers us a singular dissociation of the cerebral activity which circumscribes the field of his attention and renders him deaf and blind for what is not thereto connected. In hypnotic somnambulism, just as in a dream, we make blunders something similar to those of bees; we act very automatically, we go mechanically to an object as they go to the old place of the door of their displaced hive, without seeing what lies under our noses. Without doubt the analogy is incomplete. But it contains a large amount of truth. In the two cases it is the automatic activity of the nerve centres which predominates, leaving the plastic activity in the background. Only in man it is a question of transient inhibitions, in the insect of an impotence due to the smallness of its brain. And this impotence is evident so much the more as the localised series of acts adapted to special ends are more fixed and more complex. Thus the stupidity of the bee is more evident because it has complex instincts more fixed than most of the ants and than the wasps.

Before taking leave of Bethe's bees, I propose another decisive experiment. Let a hive be taken and carried closed (by night) to 40 or 60 kilometres at least, to be certain that the "mysterious force" cannot bring any bee to its old place. Let it be kept one or two days closed after having been put in a place sufficiently hidden that it cannot be seen at more than several metres. Before allowing any bee to go freely out, a score should be introduced into a box in some way or other and carefully marked with the same colour. Then they should be carried in the closed box to 300 or 500 metres, without being allowed to orient themselves by flying.

If I am right, they will be incapable of flying to their hive, not having been able to orient themselves in flight by vision. If Bethe is right, the mysterious force, independent of, sight will take them straight to their hive. It is necessary to have a system which allows of adapting a box to the entrance of the hive, and of making the bees enter it without any being able to fly off. Continuing, after having repeated the experiment two or three times, the bees which will be released from the hive should be marked with another colour and their flight observed going and returning.

B. ANTS.—The experiments of Bethe on ants are much weaker than those on bees. As his conclusions have already been refuted in a masterly manner by Wasmann (*Die psychischen Fähigkeiten der Ameisen*, Stuttgart, 1899, bei Erwin Naegele; Heft 26 der Zoologica von D. Carl Chun aus Leipzig), we will deal with them more briefly.

I will first recall a little-known experiment which I published in the Annals of the Belgian Entomological Society for 1886 (tome xxx. p. 137, Forel, *Études Myrmécologiques en* 1886). "Some Formica pratensis were removed from one nest to another. The removal finished, several workers continued to go visiting some plant-lice on a shrub which was on the line where the removal had taken place. Several times over I captured workers which returned from their shrub to their nest, the abdomen swollen with honey, and each time I placed them afresh on the line of the removal, but at about one metre from the spot from which I had just taken them. Recovered from their first astonishment, and after having made several very short circuits, they started off, without mistake, *en route* in the proper direction conducting them to their ant-hill, never in the opposite direction. I ask: What could be in this case the track which guided them in the midst of all the tracks of their companions going in both directions? And admitting that it might be their own track when they were going to the shrub, how could they distinguish if they must follow it in one direction or in the other, when it must have been equal on both sides, and when the fresh track which they left on the side of the bush in advancing towards their nest was no longer there to guide them, thanks to my stratagem? The idea of a track, as we ourselves make, no longer suffices here, and, as ants see badly, I think I must express a new opinion on this subject.

"In the first place it is not a question of a vague sense of the direction, for when one puts ants in a heap in a place unknown to them, and when one puts one of them two or three metres from the heap, it is absolutely incapable of finding its way to the latter. It is therefore necessary that they should know the places. But experience proves that they recognise them with the antennæ, for, deprived of antennæ, they are no longer able to guide themselves. Certain experiments of Lubbock seem to prove that the direction of the light and the shadows guide them apart from the sense of smell. But when the weather is overcast, and even by night, they guide themselves as by day.

"I begin to think that we may be here in the presence of a very important physiological and psychological fact. The organs of the internal senses (taste and smell) only bring to us, as is known, sensations badly marked, even totally unmarked in space. Herbert Spencer (*Principles of Psychology*) thinks that this is due to the fact that the nerve terminations are internal, and consequently all affected almost in the same way (confusedly) by the exciting chemical agent; whilst for vision and touch the exciting agents are localised, affecting sometimes one part, sometimes another, of the skin or of the retina. It appears there exists therein a very general truth, for we localise our impressions of cutaneous touch well, but our visceral impressions very badly. But the senses by which the impressions are localised are at the same time those which give us our knowledge of space. I think I am able to conclude therefrom that the sense of smell of insects can have peculiarities of special energy which ours has not (localisation of impressions in space). This localisation, joined to that of touch and to the memory, must be sufficient to give to certain insects this astonishing knowledge of places—impossible to explain by the vague odour of a track. The ant probably distinguishes the impressions of its right antenna from those of its left antenna, those of the left surface and of the right surface of each antenna, the impressions which come from the left side in general from those which come from the right side. Thus it distinguishes by its antennæ, and knows the two sides of the way, so that put suddenly in any spot whatever of places which are thus known to it, it orients itself with its antennæ by the objects which surround it, and knows in which direction its nest is, just as we recognise in a similar case by distinct vision and its memory (memory of places seen). The fact that man cannot picture to himself a sense of smell localising in space in no way invalidates our hypothesis. The enormous crowd of nerve terminations distributed to one or other side on the club of the antennæ is extremely appropriate to a delicate localisation."

This experiment was made and published in 1886.

It is interesting to see Bethe, who did not know of it, reach the same results, but give a totally different interpretation. He observed the route followed by the ants by making them walk on smoked paper, where they left the track of their feet. He noted that they made numerous circuits and found their food by accident, not by smelling it from afar. These facts have long been known, but for the smelling from afar it is necessary to make restrictions. Bethe has only worked on three species, two *Lasius* and a *Tetramorium*. But the acuity of the sense of smell and of the vision varies much according to the species. Further, he has observed that, on the return, they shorten their route by taking the short cuts that the track offers them where the old circuits are crossed. Thus the frequent repetition of a road makes the route more and more straight.

Then Bethe "discovered" that the track or spoor of ants is "*polarised*," that is to say that they distinguish the direction of the nest from that of the peripheral place where they go to seek their food. This is therefore exactly what I have shown very simply in 1886. But Bethe immediately sees in it a mysterious polarisation, an inexplicable force. His experiment is very pretty. He makes his ants pass on a disc capable of being turned horizontally. When the ants have passed there a certain time, he turns it 180°. Then the ants, even when the track is preserved, stop, run hither and thither very agitated on the disc; this causes an assemblage of hesitating ants, and it is only when their circuits have brought them to the other side that, again finding the track in the right direction, they continue their route tranquilly, either to the nest or to the plant-lice. The fact is admirably explained by my hypothesis, to which it gives one more support. In reality, on the turned disc the track is continuous with that of its two extremities, but in an inverse direction, right to left, and left to right. It results therefrom that the sense of contact smell of the antennæ of the ant suddenly perceives a transposition of space which necessarily disorients it, as I explained in 1886. The polarisation of Bethe lies quite simply in the recognition of the details of space and of their relational positions by means of the antennæ. We shall return to this.

Further, Bethe imagines he has refuted Lubbock and refuted me in affirming that vision does not play any part in the orientation of ants, and that the *Formica pratensis*, whose eyes I varnished, had trouble in recognising their position outside their nest only because they were suffering. Truly a strong dose of conceit is necessary to hold similar opinions regarding insects which one scarcely knows. My varnished ants behaved perfectly well and guided themselves cleverly in their boxes, but Bethe takes no account of this at all, even although I have distinctly affirmed it (*vide* page 127).

In a box, always the same, with its simple and rectilinear dimensions, the task was, indeed, very simple. But if Bethe knew ants as I know them, he would know that the way in which the blind *Eciton* guide themselves, by perpetually palpating the earth, is quite different to that in which *Formica*, which he does not know and which have relatively good vision, guide themselves. He would be doubtless very much astonished to see the way in which the American *Pseudomyrma*, with their large eyes, run accurately by rapid fits and starts on the trees, guiding themselves rather by vision than by the antennæ. In a word, he generalises *en bloc* on the three or four species of insects that he has observed, without taking the forms in which the senses have a different development.

The old experiment of the finger rubbed on the track of *Lasius*, which are disoriented by it, has been remade by Bethe with the same result, which explains itself. The smell of the finger effaces or rather covers the odours of the ants' road and momentarily disorients them.

The *Lasius* and the *Myrmica* on which Bethe has worked have the sight little developed and guide themselves almost exclusively by smell, which explains the one-sided decision of our author.

I intend to return to the antennary sense of smell, for my opinion, quoted above, appears to have been ignored or badly understood. Willibald Nagel, who alone has seriously taken it into account, has only retained that part of it which relates to the sense of smell by contact, that is to say, the chemical distinction on contact by the sensory organs of the antennary club.

But that is not the principal. Let us suppose an instant that we have in the skin of the hands a sense giving us the exact knowledge of a thousand odours and varieties of odours of all the bodies which surround us, not only when we touch them, but even in the form of very subtle emanations at a certain distance. Let us suppose these hands as rounded spindles, placed at the end of two long, mobile whips, which we have only to agitate at each step to palpate our road to right, to left, above, below. Note that if the emanations of different objects and parts of objects localised in space are confused a little by distance, the chemical nature of their surfaces is, on the contrary, very clearly localised by the limits of the said surfaces. Finally, do not forget what almost infinite variety the odours present, even to our relatively little-developed human sense of smell.

That said, see what such an organ must necessarily make us know. First it will show us by direct contact, by the surface of all the objects which surround us, quite a geographical map of odorous fields differentiated one from another, some large, others small, some round, others elongated, etc. Briefly it will give us distinct limits infinitely more varied than touch, which only gives the resistance and the contours. Put ourselves in the place of an ant in a field. One touch of the antenna will make it know the elongated smell of a blade of grass, another the rounded and different smell of another leaf, a third that of a clod of earth, a fourth that of a passing insect, and so on. If one of these odours recalls to it an object sought, it will throw itself upon it; if another announces to it a dangerous enemy, it will fly; if a third is doubtful, but seems worthy of interest, it will stop and palpate it with care. All the odorous fields distributed in the three dimensions of space will form, in its memory of perceptions, images with distinct topographical relations. Only this will be a topography of a chemical nature, with odours as the element of special energy.

But more! Our ant will feel distant emanations coming from right, left, above, below. These emanations will prolong into the air its chemical geography of space, but in a more confused way. *Its own odour, disposed on the way in the form of a track, those points touched in going by its antennæ, will have for it a precise form.* Briefly, a world of localised pieces of knowledge, with very precise relations, will be in this manner projected in its brain. If we could be endowed with a similar sense, the world would be transformed for us. The sense of smell would become a sense of forms, a source of art, of which we can only give ourselves a feeble idea.

It goes without saying that the size of the brain of an ant limits its mental activities. Nevertheless the fact is there, clear and incontestible. I am astonished that it should be so neglected.

It is therefore a question of a chemical sense which gives the exact relations between the different parts of space, very exact relations by contact, more blended, but yet very appreciable at a close distance.

This is what I have called *relational smell*, to indicate this fundamental function of an organ of smell, mobile and turned outwards, giving to its possessor relations of space by *smell-on-contact*, by specially taking account of the direct touching by the antennæ. The faculty of smell-by-contact could be called *Chemaphesthesia* and relational smell *topochemical sense*. In the language of Bethe it would be necessary to speak of topochemical reflexes, but his theory forbids him all analogy; he cannot even suppose such a thing, and to him this whole domain necessarily remains closed. For him there exists only an "inexplicable polarisation."

Furthermore, Spencer shows that distinct relations of space forms, of time sequences, qualitative differences for both are necessary to the combination of sensations, that is to say to the formation of perceptions and of associated and associable memories. It is on this account that man is not capable of distinctly associating odours and visceral sensations with his recollections. For antennary or topochemical smell, it must necessarily be otherwise.

The antennæ give us in their club, in the social hymenoptera, two kinds of regular nerve terminations, different from ordinary tactile hairs: the olfactive clubs of Leydig and the olfactive plaques of others. The clubs are hairy at the surface of the antenna and must especially come into action on contact. The plaques are flattened, scarcely elevated above the surface of the antenna, thus appearing more and more appropriate to smell at a distance. They are very developed in the Ichneumons. Among the ants, *Polyergus rufescens* possesses the most differentiated plaques that I know, but its clubs are also very apparent and very distinct.

Nothing is more instructive for the study of the way in which ants guide themselves than to observe the expeditions of the amazon ant (*Polyergus rufescens*) and those of *Eciton*, but those of *Polyergus* especially. I have made a long study thereof in my *Fourmis de la Suisse* (1874), and I refer to it for the detail. I do not understand how Bethe can pass such facts in silence and launch his polarisation theory regarding facts that can only be explained by a memory of places, by memory in general. This memory is undoubtedly especially olfactive, but the expressions "nest substance" or "family smell" are not sufficient to explain it.

In the *Riv. di Sc. Biol.* (vol. ii. No. 3, 1900), in regard to the habits of the North American ants, I have quoted my observations on the admirable faculty of orientation of a blind *Eciton*, *Eciton carolinense*. This orientation takes place exclusively by means of the topochemical sense of smell of the antennæ. Also the antennæ are in a perpetual motion, tasting each bit of ground, comrades, and larvæ. The unilaterality of this method of orientation has been pushed to an extreme perfection. When a handful of these *Eciton* is placed in an unknown spot, a long way from their nest, the geochemical map is immediately arranged and recognised at each step made by each ant with an incredible precision. When the *Eciton* has followed a line, it finds it without hesitation, without deviating a millimetre, sure of not confounding it with any other, however numerous may be the crossings. I refer to my article, and I only regret that we have no *Eciton* in Europe, for my observations could only be very short and summary.

Here in a few words is what we see in our European *Polyergus* (slave-making ant).

Incapable of tending their young and even of eating by themselves, these curious "workers" have the instinct of joining together in masses in the beautiful afternoons of July, August, and September. At a signal given by some initiators of the movement, which strike the others on their forehead, nearly all the amazons leave the nest and go off in fairly serried ranks in a given direction, with a rapidity of about one metre in 40 seconds in the grass, and in 25 or 30 seconds on bare ground. Often several starts are made without anything resulting, especially if the weather is doubtful. The phalanx, composed of about 300 to 1500 ants, advances in a fairly straight line, without hesitating. Nevertheless the ants which are at the head often return to the rear, as if to orient themselves or be assured that they are followed, so that the head of the army changes. But very often this head hesitates, searches right and left, even stops. Then the whole army scatters and searches, often for a long time, palpating everything with the antennæ. In this case the individual signals and general movements can be observed. Several ants, or perhaps only one, hesitating no longer, at last recognise the route to follow; they start off at a rapid pace, striking the others on the forehead and going off in a direction which often enough makes an angle with the preceding one. The impulse is thus communicated, and the whole army follows it, sight aiding the topochemical sense in these rapid movements of the whole. Rarely two "heads" of the army are formed at one time, each going off in a different direction. Then the army is divided into two, and each party goes to pillage another ant-hill, unless one of the heads returns on its tracks and follows the other, or loses heart and goes back. All these cases occur and still others. Several such stoppages may succeed each other in the same expedition. Sometimes they only hesitate for a moment, but sometimes also the ants cannot, in spite of long searches, succeed in finding their way, and re-enter their home empty-handed. Usually they discover a nest of *Formica fusca* or *rufibarbis*, enter it and leave it an instant after, each holding a larva or pupa in its mandibles, which they carry home with all speed. I have sometimes seen the army pass close to the side of the nest which they seek without finding it, but they rushed upon it when I had brought it to their notice by scattering several pupæ of *fusca* with bits of the earth from the nest in its direction. In the return of the army there is never hesitation; the olfactory (topochemical track) and visual memory of the outward journey is sufficient to make known to each ant the exact road. Regarding this let us note two facts. I have observed an amazon army traversing a tract of grass (which I had flooded to prevent them from passing) in spite of the water, by hanging on to the blades of grass, then cross a route swept by the dust of a violent wind, all without losing its orientation. Every head of the army wishes to be followed.

If several amazon parties in front are not followed by a sufficient troop (I have observed one exception) they return on their tracks. Home re-entered, the amazons sometimes throw the stolen larvæ to their slaves and set off again immediately to pillage the same nest once more, if it still contains booty, or another if it no longer holds any. More often they themselves bring the produce of their raid into their nest, and leave it no more that day. In fact, then, they know if the pillaged nest still contains some pupæ or if it no longer contains any. In the first case only they return to it, sometimes the same day, sometimes the next day, if the hour is too late, and this time without halts or hesitations. The fact appears to me to furnish an irrefutable proof of their memory. They must remember if the pillaged nest still contains pupæ or not, that is to say, if there were many or few. Neither reflexes, nor odours, nor polarised tracks can explain the thing, and I have never seen *Polyergus* pillage a nest several times running which did not contain more pupæ.

I have watched during a single summer (1873) 44 expeditions executed in 30 afternoons by one single colony of *Polyergus rufescens*, and I have calculated that these ants must have carried off to their home close on 29,000 pupæ of slaves in this one summer.

How do *Polyergus* discover nests of *Formica fusca*, situated often 40 or 60 metres from them and well hidden? In the springtime and on summer mornings the *Polyergus* workers go out individually from their nest and explore the environs to great distances, thus discovering the nests of the species which they pillage. One can admit with certainty that it is these explorers which become later the initiators of directions, both at the setting out and afterwards at the halts of indecision of the army. And it is thus that the antennary topochemical sense of smell plays its part. At the time of a halt, one of the workers which are searching finds, thanks to its topochemical memory of places, the landmarks which orient it, and goes off carrying the others in its train. I think, with Lubbock, that sight helps the orientation of *Polyergus*, but Fabre has enormously exaggerated its importance. Deprived of its antennæ, a *Polyergus* can no longer orient itself.

Without having, it seems, had knowledge of my experiments, Fabre (*Souvenirs entomologiques*, 1882) has attempted to throw out the amazons on their return by placing sand on their road, by inundating (as in my case), putting the scent of mint on their route, finally by putting paper upon it. The amazons hesitated, searched, but ended by getting over the obstacle and finding the right road again. I have made some quite similar observations. That shows that their sight helps them to orient themselves, but by no means that it alone orients them. And Fabre completely forgets that the returning ant knows and feels by its track *from what side it comes*, and necessarily infers from it that it must direct itself in the opposite direction to re-enter its home. Reaching an interruption (Nature forms one sometimes), it hesitates, then, understanding what is the matter, inasmuch as the tract behind will lead it to the pillaged nest and not home, and that there is no other, remembering further that it passed by that way a short time previously, does not hesitate to cross the interruption by continuing at a venture the direction of the track it has been following. And, indeed, after the obstacle, it finds the track on the other side. I am persuaded that one might end by disorienting the army if one interrupted its track over a great length, by covering, for example, the grass with sand for twenty or thirty metres. But then, in searching, the ants would turn round the obstacle, and would end perhaps by finding on its outskirts some other track known to them.

What is left of Bethe's unknown force and of his polarisation with regard to these facts?

Fabre grants that it is the memories of places which guide the amazons. He makes some charming experiments on *Pompilus* by changing each time the place of the paralysed spider that these insects lay down, and showing that they always find, without hesitating, the last place (what does Bethe say to this?). He also grants them the memory of places. Why does he refuse it to his *Chalicodoma*? Singular inconsequence!

If the sense of smell does not furnish man with memory images, it is, as Herbert Spencer has shown, because of the absolute incapacity of the whirlwind of odours to be grouped in precise relations of space or of coexistence on the olfactory mucosa of our nose, and consequently to form recollections clearly associated in our brain. *For the topochemical sense of the antennæ it is quite otherwise. The precise relations which it gives in space must necessarily furnish associated perceptions and precise recollections of parts of the space travelled over in succession or in juxtaposition to every brain capable of storing them up.* It ought even to furnish relations of sequence or of time, more precise than those which our sense of smell gives us.

It is in no way a question here of an hypothesis in the air, but of palpable and absolutely certain facts. Only, to understand them, it is necessary to study the psychology of the senses. With Bethe's leave, comparative psychology reserves for us, still, numerous lights in this domain, of which he closes the door by his prejudice.

Summary of the Faculty of Aerial and Terrestrial Orientation at a Distance of Insects and Higher Animals, as well as of the Antennary Topochemical Sense

The faculty of orientation outside the body itself of the individual rests neither in a special mysterious force, nor in an unknown sense, static, geotropic, or other, nor in a sixth sense, nor in the semicircular canals. It is the result of the experience of known senses, combined or not, especially of sight and smell, according to the case and the species. In aerial orientation, it is vision which most predominates. The case of the carrier-pigeon constitutes the most surprising case of aerial orientation. Since it is explained by vision, it is idle to search in the domain of other mysterious causes. In terrestrial orientation the sense of smell often plays a predominant part, but gives place to sight in many animals, among which are man, monkeys, arboreal reptiles, certain insects, etc. In the orientation of subterranean and cave-dwelling animals, smell and touch reign as masters. In spiders, it is touch which is the principal orienting sense. We shall treat later, in a chapter apart, of orientation in aquatic media.

Nevertheless it is necessary to recognise that certain senses undergo in the animal series considerable morphological and physiological transformations which greatly modify their quality and the kind of knowledge which they obtain. Such is the case for *vision by faceted eyes*, and for *the topochemical sense of smell of the antennæ, as much on contact as at a distance*. As our palate is the seat of a sense of touch as well as of taste, so the antennæ contain, as well as the topochemical sense, a topo-mechanical sense of touch. The aerial orientation of bats merits further special study.

CHAPTER XI

ORIENTATION IN SPACE (*continued*)—FACULTY OF COMMUNICATION, MEMORY OF PLACES AND OF TIME IN BEES

H. VON BUTTEL REEPEN[1]

WHEN writing Chapter x. I was ignorant of the work of H. von Buttel Reepen. If on the one hand I regret it, on the other it has the advantage of having rendered my criticism of Bethe independent of his, and the reader of both works will be astonished to see to what point our results agree. This agreement gives an even stronger basis to our results. M. von Buttel is an experienced apiculturist, as well as a zoologist, which adds infinitely to the value of his work, and for this reason his opinion and statements concerning bees are very much more valuable than mine. I owe him reparation for my omission, and I make it with the more pleasure because my results agree with his, save as regards hearing, which he thinks may be attributed to bees. His work is divided into chapters, which we will analyse as briefly as possible. This masterly work having appeared in German, I think that an analysis will not be superfluous.

Odour of the Nest and the Reactions which it causes

Von Buttel repudiates, as I do, the terminology of Bethe, and distinguishes the following odours received by bees:—

1. *Individual Odour.*—V. Buttel shows by the help of a

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[1] Buttel-Reepen, H. von, *Sind die Bienen Reflexmaschinen?* Leipzig, 1900, Verlag von Arthur Georgi. *Idem*, Biolog. Centralblatt, Bd. xx., 1900 (the same article with several modifications).

great number of facts that the queen-bee has a very strong odour, especially strong at the epoch of laying, and different for each queen. The workers distinguish the queens one from the other by the odour, kill those which are not theirs, and only become habituated little by little to a new queen. The court which they pay to their queen depends on her odour and diminishes with it. If, therefore, the queens have each an individual odour, it must be admitted *a priori* that this is the case (probably less marked) with the workers. I may add that this conclusion of V. Buttel confirms me in my supposition of an analogous fact among ants.

2. *Family Odour.*—All the young of the same mother have an odour common to the family.

3. The smell of the larvæ and of the bee-bread.

4. The smell of the males or drones.

5. The smell of the wax. This odour is complicated with the combination of the individual odours of the bees of which the wax is a secretion.

6. The smell of the honey.

7. The smell of the nest is in the normal state a mixture of the six preceding odours or of part of them.

But twenty-four hours suffices to cause the acceptance of a strange queen by a queenless swarm (the queen is protected during this time by shutting her up in a piece of gauze in the centre of the hive), and this swarm may be made up by taking bees from thirty different swarms.

Therefore the odour of the nest is not innate. It consists of a mixture of individual or family odours combined with the other odours.

When two hives are placed one beside the other and the queen and all her nursery is removed from one, it often happens that all its inhabitants go joyfully to the neighbouring hive; here they are well received, and not killed or maltreated, as ought to be the case if the "chemoreflex" of the nest was not susceptible of modification, as Bethe supposes.

When a hive allows itself to be pillaged of its honey, instead of expelling the pillaging bees, the enmity of its inhabitants may be excited afresh towards strangers by the help of certain methods (fermented honey, etc.).

Bees which return with the crop full of honey are usually well received, even by a strange hive: to propitiate its inhabitants the honey is disgorged and offered to them. By exchanging the place of a strong hive with that of a weak hive whilst the bees are foraging, the second can thus be strengthened.

By sprinkling the population of two hives with an odorous substance or flour, one can unite them without danger of battles. Bees lose their memory of places when they are narcotised with saltpetre, ether, etc.

In the opposite direction, perversions of instinct may sometimes be observed: bees kill their companions as these return from foraging, or even their queen. Is this due to abnormal odours?

The very characteristic smell (even to man) of the brood of bees, which produces by its metabolism a fairly strong heat, strongly attracts bees and suffices to hold and fix in the hive a naturally vagabond population.

Bees sacrifice everything to their queen, and feed her when they are themselves dying of hunger, to such extent that they all die, and the queen alone remains alive when they have been left fasting.

The queen does not react to the smell of the nest, neither in a hostile nor in a friendly fashion. She never shows herself hostile to a foreign worker. She asks and receives her food from every bee, friend or enemy, even when she begs it through the openings of the gauze of workers who seek to kill her by assailing her. Thus a queenless hive will feed twenty or thirty queens confined in gauze; but when they have adopted one they will leave the rest to die of hunger. The queen has only one enemy: her competitor, usually her daughter or her sister, which has the same odour of the nest and family as the reigning queen. When they enter into contest, one of them nearly always is left on the ground.

In very rare cases one has seen two queens living in peace side by side in the same hive and on the same eggs.

The drones are international and are admitted into all hives up to the time of their Saint Bartholomew (general massacre).

When the worker bees, for want of a queen, themselves commence to lay eggs (male eggs), it becomes more and more difficult either to make them accept a queen or to get them admitted into another hive. They are killed there. That comes, according to Dönhoff, from a progressive change in the composition of the smell of the nest.

From all these facts, and others which would be too long to quote, it results that the odours of individuals, males, queens, family, and nest, are really infinitely more complicated than Bethe imagined, and that the same is true of the various reactions which they cause.

Faculty of Communication of Bees.

This faculty is denied by Bethe with his usual assurance. V. Buttel is not of this opinion, and backs his views with very interesting experiments.

He first calls attention to a mistake of Bethe. Bethe confounds the plaintive cry (*heulen*) of bees which have lost their queen or which are scared, with their joyful buzzing (*sterzeln*) when they find their hive or their queen. The "cry" has another sound, prolonged, acute, and plaintive, while the joyful buzzing is shorter, lower, more humming, and is combined with a raising up of the posterior segment. Frightened or angry bees take an attitude which resembles that of the buzzing of joy, without being identical.

When the queen is taken away from a large hive of 50,000 to 60,000 bees whilst they are hard at work foraging, they often pass an hour or even several hours before they find it out. Then, almost suddenly, the hive changes its aspect; the joyful buzzing is changed into a "cry." The bees are agitated, terrified, as if seeking something everywhere, and become angry, disposed to sting, both inside and outside the hive. In small hives the trouble usually begins as soon as the queen is taken away, especially at the times when the bees are not foraging. How, therefore, do the bees recognise the absence of the queen?

It cannot be by smell, for on the one hand the odour of the queen is persistent and permeates the whole hive, and on the other more than an hour is often necessary before the workers note her absence. When they remark it, it is almost suddenly. And if Bethe was right in attributing everything to smell (chemoreflex), that would prove that he was wrong in this smell to be that of the nest, with which the queen would be impregnated, seeing that then, on the contrary, all the reaction would proceed from the odour of the queen which would dominate that of the nest.

Neither is it the escort of young bees feeding the queen, her "court," which, remarking her absence and, searching for her in vain, make it known to the remainder of the hive, for the said escort can be removed with the queen and the effect is the same. Further, a hive can be formed artificially with old bees without a queen. The "cry" is produced there. When any queen whatever is put there, caged, the hive is appeased as if by enchantment, and the bees start to buzz joyfully.

Having crushed the queen of a swarm by accident, and fearing that the swarm would disperse and would re-enter its original hive, V. Buttel pinned the crushed queen on a bit of cork and placed her thus in the swarm. The swarm remained tranquil, worked at the honey, and the ordinary court continued to surround and lick her defunct majesty.

But further! V. Buttel placed a caged queen in a weak hive from which he removed all the combs, thus turning it into a simple swarm. Next day he took away the cage with the queen. Soon the "cry" and the typical agitation broke out. Then after having removed the queen from her cage, he rapidly placed the latter (empty) in the midst of the bees. Immediately the "cry" ceased, and the empty cage was assailed by bees buzzing for joy. Therefore—the experiment is clear—the simple smell of the cage where the queen had been was enough to pacify the bees.

But then what happens in the first experiment where the removal of the queen is enough suddenly to cause the "cry," when her odour must persist?

Von Buttel very judiciously deduces from these facts that there is more in it than simple odours. He says that in the last case the sudden appeasement by means of an empty cage has to do with an instinct rendered acute by the urgency of a grave and precarious position. The simple memory evoked by the smell of the queen was then enough to appease the workers. So, says von Buttel, in regions poor in pollen, one sees in the springtime bees pressed by want load themselves with the dust of coal, bricks, or barns. That does not mean that they confuse the two things, and when they have their true queen or real pollen they abandon their empty cage and coal or brick dust.

We will add that it is the same story as that of the fowl from which the eggs have been taken and which sits on a white stone instead, and as that of the old maid who attaches herself to dogs and cats for want of children (see E. Rambert, "The illusions of the heart"). How striking is the analogy of these facts and those which I have related in my *Fourmis de la Suisse*, pp. 263 to 274 (exp. v. Nos. 1 to 10), regarding the relations of adult ants of various ant-hills, which fight almost to extermination or ally themselves according to the circumstances.

They fight whenever they (the two parties, or at least one of them) are at home and at their ease. They ally themselves when both parties are in a very precarious position.

A little reflection shows that it is a question in all these cases of psychic and psychosensible antagonisms, in which the qualitative and quantitative differences, concerning either the sensory stimulating agent or the instinctive or plastic cerebral dynamisms awakened by it, are reciprocally in play. Let us explain.

The bees require a queen to be satisfied ; it is an adapted instinct. She is taken from them. A slight diminution of odour and of other signs (absence of the humming and of the movement which take place round the queen on the part of her court) draw the attention of some bees thereto, which are assured by their senses that the queen has disappeared and then instinctively give play to their painful emotion by their "cry." Von Buttel thinks that this "cry" is "heard" by the other bees, who are then rapidly contaminated by this "panic." It matters little whether it is a question here of true or false audition (we shall return to this). The fact that the cry is communicated, like the panic among ants (see *Fourmis de la Suisse*, p. 315, exp. ix., and p. 359, exp. xxi.), clearly proves that there is communication of an instinctive emotion by the channel of some sense or other. This emotion can take on the character of joy, fright, anger, and discouragement among bees as among ants. These are anthropomorphic terms, I admit, but I do not know how to find any that better convey the facts and their consequences. Let us rather say that they are "bee-like" or "ant-like" emotions and not human, to avoid all misunderstanding on the subject. To resume the emotion of the "cry" puts the brain of the bee in an increasing state of dissatisfaction, that is to say of trouble. As von Buttel has very well pointed out, to call up, however feebly, an agreeable recollection by the sense of smell (empty cage in which the queen had been) then suffices to calm by contrast the nearest agitated bees which will perceive the odour. The calm will then be communicated to others, as the "cry" was communicated. On the contrary, the same cage, when found empty, will provoke the "cry" if previously it has contained a queen, in a hive, because here the contrast will have taken place in the inverse direction. So the same morsel of mouldy bread will disgust the sated Dives and will delight a poor famished wretch. All is relative in psychology, and a striking agreement is seen between the psychology of the sentiments or emotions in the insect and in ourselves.

We say that all is relative at the same time that all is contrast and antagonism quantitative or qualitative, or both combined, in what determines the emotions and actions of insects as much as our own. We have just given a striking example thereof quoted by von Buttel. Similarly we have seen elsewhere (third part of these experiments, in connection with Plateau) the impressions of honey and their associated memories efface and replace those of the dahlias, and again I have seen (*Fourmis de la Suisse*, p. 446) the instinct of the defence of the ant colony (of social duty!) prevail over gluttony, that is to say, over the desire to eat honey, among ants. In these antagonisms it is sometimes a direct sensation of one and the same sense which prevails over another by its intensity or its quality, sometimes a memory of combined sensations or perceptions which prevails over an actual sensation or perception, sometimes a complex emotion or instinct which triumphs over all the actual or antecedent sensations or perceptions. These are the fundamental psychological elements which the attentive observation of the social insects discloses to us. It is necessary to be blinded by bias like Bethe not to recognise them. I repeat again that instinctive automatism takes the lion's share, but there are in every difficult or exceptional circumstance, however little this varies from the normal, intermingled spurts of plastic adaptation.

Let us return to von Buttel Reepen.

Von Buttel removed the queen of a swarm at the moment of its departure. Usually in such a case the bees of the swarm seek in vain and re-enter the hive (that is to say the absence of perceptions relative to the queen prevents the full development of the instinct of swarming [Forel]). In this particular case, nevertheless, the swarm went quietly to suspend itself in a cluster on the branch of a tree, as if it had a queen. The examination of the hive proved that there was not an open royal cell which a young queen could have left. In the end the swarm, after resting quietly for half an hour on the branch, suddenly dispersed, flew from one place to another, and then finally re-entered the hive; certain proof that they had no queen among them. Here the instinct was displayed for half an hour without adequate perceptions of the queen, probably by simple prolonged imitation by the workers. What is curious here is the tranquillity of the queenless swarm.

But von Buttel points out that in the free air the bees have difficulty in perceiving the odour of the queen. It is, indeed, necessary to keep a queen in her cage in the middle of a free swarm a very long time before the bees know the queen, and even so one often fails. But as soon as a bee alights buzzing joyfully on the royal cage, the other bees, attracted by its joyous buzz, imitate it and the swarm is pacified and alights.

A rule of apiculturists consists in caging the queen at the moment of the great flowering time, in order to hinder her from laying at this moment and thereby to increase the harvest of honey by diminishing the hungry mouths of the hive. But in thus disarranging the normal instinct of the bees, another result is often reached: the bees act as if they no longer had a queen and make royal cells at an abnormal time (as when their queen becomes old and sickly). Von Buttel thinks that it is a question of an unsatisfied instinct of feeding. The workers have too much nutrient juice and feel the necessity of using it (or also the caging of the queen produces in them, by contrast, a negative effect or of relative diminution of the antecedent normal perception of the free queen; or better still, both causes combine [Forel]).

Von Buttel removed the queen from a strong hive full of eggs, bees, and honey, a hive opening from behind and allowing of working in the upper tier where the honey is found. When the agitation and the cry of the bees had reached its height, following the removal of the queen, von Buttel replaced her in a cage above, on the honey tier, and immediately observed the bees which were at the other end, near the door of exit, and which were separated from the replaced queen by all the mass of eggs and bees of the hive. Almost instantaneously the cry ceased everywhere at the same time, and the bees which were near the exit hole began to buzz joyfully, raising the abdomen.

Experimenting in the opposite direction, von Buttel hung the cage containing the queen on a staff which he stuck in the ground, so that the cage was situated at the height of the door of a hive and 35 cm. therefrom at one side. None of the bees going out were capable of smelling the queen, and the hive remained in agitation, continuing to cry.

From these two classes of facts von Buttel concludes, doubtless rightly, that it is not the sense of smell alone that causes the sudden repose of the bees, and that another sense, more acute and of more rapid communication, publishes to them good or bad news. Sight is excluded by the above experiment. Von Buttel concludes it is hearing. The tone of joy (buzzing) calls the companions or tranquillises them; the moaning tone of the plaint, the "cry," stirs them and makes them forget the work. Von Buttel gives other proofs of the hearing of bees. He points out the special tone which they give out when they swarm; they are then possessed by an enthusiastic emotion which turns their attention from everything else; they forget all, even their hive, and even to sting.

When before swarming a few bees hang beard-like in front of the hive, suddenly several bees are seen to go out of the hive, throw themselves on to the "beard" and push themselves with lively force, displacing the others. At this signal (von Buttel supposes that it is a tone which we do not hear) the beard dissolves, the bees rush into the hive, gorge themselves with honey there, and leave suddenly an instant later to swarm. Von Buttel quotes after facts showing that the swarm attracts other bees near by, which he attributes to the "swarming tone" which is given on the wing. Then he shows how the trapped swarm is brought into a hive by shaking a few bees near the door of the hive. They enter it buzzing. According to von Buttel it is this buzzing that makes the others turn round and follow them. Let us remark in passing that von Buttel takes no account of sight in the aerial movements, and even in those last mentioned on the ground, which is wrong in my opinion.

Then von Buttel describes what passes in the strong hives which require to swarm several times, and in which the workers prevent the young queen first hatched (after the departure of the old queen with the first swarm) from killing her contemporaries still enclosed in their cell or cocoon. Nevertheless the latter do not dare to come out, fearing the sting of the young queen. They content themselves with cutting a small hole in their prison to pass their proboscis through and thus be fed by the workers. The young queen, jealous, marches about, presses her head against the comb, and gives vent to a prolonged sound: *thute*, *thute*. The enclosed queens reply by a deeper and shorter tone: *couak*, *couak*. This alternation of tones may go on for hours, even for days, if rain prevents the second swarming.

Finally, when a strange queen is placed at liberty (not caged) in a queenless swarm, the bees nearest to her fling themselves upon her to bite and sting her (foreign odour). The queen escapes, but is pursued. Then, in her terror, she utters "cries of fright" which disturb the whole hive. The disturbance of the hive is, indeed, not produced when the queen is caged and does not cry. Von Buttel concludes therefrom that the workers hear the queen's frightened cries.[1]

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[1] There is in this a curious point of the psychology of the bee which von Buttel does not notice. How is it that this same caged queen, of which the simple presence appeases and "rejoices" the hive distracted by the loss of its queen, will be attacked, stung, and killed when she is not caged? There is in this a remarkable psychological contradiction, very characteristic, in my opinion, of the instinct and of the weakness

I confess that the judicious remarks and the experience of an observer so excellent as von Buttel Reepen make me seriously doubt on the question of hearing in insects. Nevertheless it fails to convert me on a fundamental point: where is its organ, if it exists as a special sense, for special energy? We know and prove without difficulty the organs of other senses. Why not that of hearing? So long as its seat and the deafness consecutive to its extirpation have not been demonstrated, there remains a possibility that even von Buttel cannot exclude, that of the "false audition by touch" of Dugès. I have shown elsewhere how insects, so light and so small, are easily impressed in their tactile organs by the least vibrations of the atmosphere and of the bodies which sustain them. But precisely those of the experiments of von Buttel which peremptorily exclude sight, that is to say those which are passed in the darkness of the hive or across its contents, in no way exclude the tactile perception of vibrations. And those which seem to indicate an audition at a distance in the open air do not exclude vision. The differences of the tones emitted by bees, differences which we perceive by our hearing, might very well be perceived by them as differences of tactile vibrations, according to their amplitude, as we ourselves perceive very deep sonorous vibrations by touch, and not only by hearing. There is here a very hard

of plastic adaptability in these insects. Indeed, our artificial hives submit the instincts of the small bee brain to rough tests to which Nature has not adapted it. In Nature, every swarm leaves with the queen of the hive, who is replaced by the contemporaries not yet hatched at the time of her departure. A hive which loses its queen without having the eggs to replace her is lost; it disperses, and the bees must gain entrance elsewhere or perish. No one brings them a caged queen to accept. They are not adapted therefore to this artificial case. The caged queen produces in consequence the conflict of two natural instincts: (*a*) enmity against every odour of a foreign bee; (*b*) joy due to the return of a queen. If the foreign queen is not protected, the struggle and her cry inflame the disturbance and make (*a*) triumph. The cage, by preventing the struggle and the cry, make the instinct (*b*) triumph. Further, it prevents the more intense perception of the contact-odour (topochemical perception), and this is probably what keeps the worker bees from being irritated. Little by little the mixture of odours takes place in the hive; the bees become accustomed to the emanations of the new queen, instinct (*a*) is effaced, and the cage becomes useless. According to von Buttel, it is hearing which makes known, if not awakens, the first instinct (*b*). The deliberate individual combats of ants offer facts of analogous nature, such as the individual hatreds kept up and inflamed by repeated conflicts, and the exceptional alliances on account of friendly services rendered to natural enemies (Forel, *Fourmis de la Suisse*).

question, which must be put. But whether we are dealing with hearing properly speaking or not, the fact that bees communicate their impressions and their emotions has been victoriously demonstrated by von Buttel against Bethe, and confirms what I have observed in ants.

Memories of Places in Bees.

It is in this chapter that my observations agree with that of von Buttel in refuting Bethe. Von Buttel declares, as I have done, that Bethe confirms by his experiments the memory of bees for places, when he believed that he was refuting it.

At the very outset von Buttel establishes what I have said, that is, that there is no fixed "aerial route" for bees to a hive. They set off in the direction where they find foraging, whatever it be, and return by the same. That is observed especially well in the open. When there is foraging in several directions, they are distributed in consequence.

Further, von Buttel declares that Bethe is deceived as to the distance at which his "unknown force" acts. Indeed, it can act up to six and seven kilometres, when there is nothing to pillage in the surroundings of the hive, but much on the contrary at these great distances. The distance at which they orient themselves depends simply on the space which they have learned to know in their flight.

Bethe is deceived, says von Buttel, in saying that the line of bees is more or less ascending according to the weather. He makes a mistake in saying that this "line" always leaves the hive in the same direction as the cardinal points, which would almost always be south, east, or south-east. This error is due simply to the fact that the town of Strasburg is situated to the north of Bethe's hives. Bethe is further deceived in thinking that his bees did not know the town of Strasburg. Von Buttel here gives the same reasons as I, and adds that, at the time of their first going out, which serves only for their orientation, the bees fly in every direction to orient themselves everywhere. Von Buttel again declares more energetically than I that Bethe's bees must know Strasburg at the small distance of one kilometre. He quotes on this matter K. Zwilling, editor of *L'Apiculteur d'Alsace-Lorraine,* who describes how the bees of hives situated against the ramparts of Strasburg go to pillage the sugar of the *Fabrique de Bonbons Pale*, and even go right into the Place Kleber, in the middle of the town, naturally at the time when there are no flowers. Others go to flowering trees in the town and to the flower-market.

As regards the bees released by Bethe in the streets of Strasburg and taking "exactly the direction of their hive even before they had raised themselves to the height of the roofs," von Buttel reduces it to an absurdity by showing that many of the said bees took far too long a time in their return flight to have flown directly to the hive; further, that the bee leaving a dark place such as a Strasburg street always flies first where there is the strongest light, which, according to Bethe's indications, must come precisely from the direction of his Institute (situated in the south, the town being in the north; Bethe released his bees on a sunny day).

Von Buttel observed that bees narcotised with ether, chloroform, or saltpetre lose for ever all the recollections of places acquired before the narcosis. They no longer find either their way or their hive, and no longer recognise the other bees. One can put them in any hive one pleases. He concludes therefrom that they possess memory, for one cannot *forget* without having had a memory! This is indeed the most simple and most conclusive proof. The unknown force of Bethe consists precisely in the memory of bees. Recovered from their narcosis, the bees learn everything afresh, the way to their hive, that to the flowers, etc. Therefore they "learn," which Bethe denies.

Von Buttel points out, as we, how absurd it is to postulate an unknown force after the experiment made on bees carried from a distance, in the course of which most of the bees released elevated themselves and flew to the hive, whilst two, which did not know how to orient themselves, returned to the starting-point. The "unknown force" must act for all alike. I shall not dilate on the refutation of those of Bethe's experiments on which von Buttel argues like me. But he further points out that the suggestion of an "unknown force," impelling the bee far from its home in two different directions at once, on the one hand to its hive, on the other to the box from which it has been released, contains a flagrant contradiction. I add that, according to the parallelogram of forces, Bethe's logic ought to drive the bee by the resultant in a direction intermediate between the hive and the departure box. This is no mere pleasantry, if we grant Bethe's ridiculous mechanism.

Von Buttel repeated the experiments of Bethe on bees brought from a distance. His results differ from those of Bethe. He had taken his bees (from two hives) in two boxes (call them A and B). He released the bees A by opening their box on the grass and getting them out rapidly. The bees raised themselves to about three metres in a spiral, turning their heads towards the starting-point. Two only returned to the box. Von Buttel took it away. The bees flew and searched all round the starting-place. Suddenly the bees which were in box B, in his pocket, began to buzz. Immediately the bees A (having heard them, von Buttel believes) began to buzz round von Buttel and to follow him as well as their companions wherever they went. Even when von Buttel replaced the box A at the starting-point, the bees A paid it no further attention.

The second box was lifted in the air with the hand, and the thirty or forty bees which it contained released. They described circles around the box. At the end of half a minute von Buttel withdrew the box and retired, trying to note the place in the air where the box had been. But two bees alone returned to it. The mass of the swarm, searching to right and left, ended by reuniting at the end of several minutes in circles more and more concentric at about two metres from it, almost to the level of the ground, *i.e.* at a height exactly equivalent to that of the door of its hive! Von Buttel is persuaded that it sought the said door. A certain time after, the bees dispersed, then began to follow von Buttel and his companions up to about twenty paces' distance, in the direction of the house.

Certainly these observations are curious and show where Bethe has observed badly and dogmatically. But von Buttel will here allow me one observation. Elsewhere he repudiates the common opinion which attributes to bees the faculty of recognising their keeper.

Doubtless he is right to deny the anthropomorphic sense usually attributed to this recognition. But if the bee is capable of recognising a locality, its companions, its hive, and its way with the help of vision, of smell, and (according to von Buttel) of hearing, why should it not recognise this great mobile being who occupies himself so much with it and who, without any doubt, must leave it constant visual and odorous impressions, as long as he keeps the same clothes? Doubtless his mobility must render his recognition more difficult to bees, so used to orient themselves on fixed objects. But it seems to me that the above experiments, especially the second where the hearing of bees buzzing in a box no longer comes into account, speak precisely for the common opinion. Von Buttel will tell me that the bees also followed his companions. I do not wish further to suppose that they usually distinguish one man from another. But von Buttel himself pointed out that bees thus disoriented and distracted are perplexed and are bad subjects for experiment. I here make a restriction and I say: *bad for normal instincts, but admirable for the faculty of plastic adaptation!* That said, I conclude that bees in a normal state, around their hive, will have very good sensory reasons for distinguishing their bee-keeper, their "papa," in his ordinary clothes, from a stranger. There could be some pretty experiments made here before deciding the question. It goes without saying, once more, that I speak of a "bee-like" and not "human" distinction.

But the *experimentum crucis* of von Buttel is the experiment which I have "proposed," without knowing that von Buttel made it in a still more simple manner: 1. It was enough to take young bees, those which fed the queen and had not yet taken their first flight of orientation, and to carry them to a *minimum* distance from the hive. None of them knew how to find the way back to the hive. But it was not because this faculty was itself wanting to them. It is true that for the first fifteen days of their life the young bees are as a rule exclusively occupied in feeding the queen and the larvæ. But if one forms a hive exclusively of young bees, they already begin to forage on the fifth or sixth day following their hatching and find their way back as well as the others.

2. If old foraging bees are taken even very far from their hive, they all return to it, without exception.

3. If a hive be carried to more than seven kilometres from where it was, and when old bees are carried, before they may

have been able to take their orientation flight, to 80 or 40 metres only from the hive, they are incapable of finding it again, however little it may be hidden from them by trees, houses, or bushes.

4. Von Buttel carried a hive to two kilometres from where it was, without narcotising the bees, and placed an empty hive with empty combs at its original place. Several hundreds of bees returned to the old place and flew frightened around this empty hive, in spite of their perfect liberty to return to their own transported hive.

From these absolutely clear and irrefutable facts von Buttel concludes that bees obtain memory of places by visual orientation. He consigns the hypothesis of Bethe's unknown and mysterious force absolutely and irrevocably to the realm of absurdities.

Von Buttel again points out that bees which have swarmed appear to have forgotten their old hive, for they no longer return to it. In reality this is not the case, for if one takes their queen away within several days of the foundation of the new hive, they will return to the old one. It is here, therefore, a question of new and very strong associated representations furnished by the swarming which immediately takes them out of the old ones (those of the old hive). But these latter are not effaced as after narcotisation. Another effect of concurrence of forces.

Von Buttel points out certain agents which weaken the memory of places in bees, as buckwheat honey, darkness lasting several days, cold, baths in water, finally, lapse of time. At the end of five to six weeks, in summer, bees have absolutely forgotten their old localities, including therewith the old place of their hive (this is easy to see by replacing them side by side). But this rapid forgetfulness only takes place if new impressions come to efface the old ones. When a hive is displaced in the spring, before the first outgoing of the bees, it may be noted, when the warmth comes abruptly, that the bees return to the old place where the hive was the previous autumn. J. Huber saw, even in spring, the bees return to the window where they have been given honey the autumn before. Here again Bethe, who declared the contrary, is refuted.

Von Buttel then shows that bees associate their recollections. Some bees came in a body through his window to eat some honey from a comb which was in his room. Chased therefrom, and the window having been closed, they began to seek in every surrounding room of which the windows were open, even in the opposite house. My experiments quoted in regard to Plateau (third part of these Experiments and Remarks) agree absolutely with these facts. But in all these cases and in all those where bees, wasps, etc., returned several days after to the spot where they had been given honey or flies, even when there was no longer any there, it could only be a question of memory associations, since the chemoreflex or photoreflex stimulating agent was no longer there to attract them. Von Buttel very well points out that a plant will never react further in a heliotropic or chemotropic manner when the stimulating agent ceases to act directly upon it.

Buckwheat only gives honey in the morning. The bees fly to it till nearly ten. They return to it again two or three times to no purpose, then cease to go there after ten o'clock. Experience teaches them little by little to go there only in the morning, even when the smell and colour of the flowers are always there to attract them.

One extremely curious fact is the instinct of scout bees which go, before the swarming of the old queen, to considerable distances from the hive (several kilometres sometimes) to seek a suitable locality for the swarm which is preparing. When this takes its flight, they serve it as guides and conduct it to the place which they have chosen. According to von Berlepsch (1852) and von Buttel the fact is absolutely certain and shows afresh the memory of places. Out of more than 50,000 bees, there are not more than 50 to 100 which act as scouts.

The old bee goes off straight from the door of the hive. The young bee, which leaves for the first time, first orients itself by describing circles round the hive, towards which it always turns its head. Thus the bee learns.

When bees are deceived by displacing their hive to a very distant place, they set off at once when their door is opened, instead of first orienting themselves like young bees. If the weather is cold or windy, many are lost. If it is calm, they find the hive again by orienting themselves from point to point on the return by vision.

But if there are several neighbouring hives, they do not distinguish their own and are obliged to examine several hives by the help of the sense of smell before finding it again. This is, therefore, yet another interesting fact which contradicts Bethe absolutely.

Von Buttel shows that the experiment where Bethe carried a hive to a distance was very badly done. Ordinarily, even for their longest flight, the bees never stopped more than an hour away from their hive. Bethe made them return at the end of five or six hours. That proves simply that the first parties were lost. Bethe appears not to understand the normal flight of orientation of bees.

As regards the plane tree cut down by Bethe, von Buttel points out that bees scarcely live six or seven weeks in summer,[1] and consequently the reason whereby Bethe's bees "continued to fly upwards, as if the tree had been still there," fourteen weeks after it had been cut down, could not be a fixed habit, nor a "bee-line," since they could no longer be the same bees.

Von Buttel, discussing the instinct of bees of orienting themselves exactly in space, especially in elevation and on an exact point, not at first by the direct vision of this point even, but by the relative position in space of large surrounding objects and especially of the ground, concludes therefrom, as I, orientation by vision and the uselessness of the experiments where Bethe hid the neighbourhood of the hive by various objects. The bee orients itself on a large scale and at a distance in its rapid flight; that goes without saying. When it is resolved upon finding the place even of its hive after it has been removed, it is evident that objects placed in front or to the side will not prevent it from finding the hive, which has not altered its position. To conclude therefrom the absence of memory images in the bee, as Bethe has done, says von Buttel, is anthropomorphism of the first water, and we say so with him. Indeed, it is to require of the bee human reflections and a human vision.

As a matter of fact the bee, oriented in the country, flies straight to the place where the door of its hive is without noting the surrounding objects. But, arrived at this place, it stops and searches buzzing, if unexpected changes strike its attention. The more busy it is, and, thereby, absent-minded, the less it notices the alterations which have occurred.

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[1] The reader will note that, a few paragraphs above, the author remarks that "At the end of five or six weeks, in summer, bees have absolutely forgotten their old localities."—Trans.

When a bee is released in the air at twilight, not far from its hive, it describes several circles and falls, lost, to the ground. It can no longer orient itself, for want of light. What is become of the "unknown force" of Bethe?

A bee-keeper (Dathe) had 500 hives. In some of them the door was turned to the south, in others, close by, to the east. When the clouds accumulated before a storm, the bees returned frightened in all haste to the hive. Then they often made a mistake as to the hive because of their hasty rush for shelter. Indeed M. Dathe saw on such an occasion numerous bees belonging to hives facing to the south rush on the south wall of hives facing to the east and seek their door thus vainly. An error in orientation by sight, quite explained by too great haste, says von Buttel. How is it to be explained by the unknown force of Bethe?

As regards colour vision, von Buttel quotes two striking cases. The neighbour of a bee-keeper painted the upper façade of his house sky-blue. Till then the bees flew over the roof towards the blue sky. The sky being covered after the painting of the façade, the bees, deceived by the colour, started to rush against the blue wall, thinking to fly skywards! A weak swarm of young bees which left a hive painted blue were upset by the play of other stronger swarms gone out at the same time. Dispersed in several small detachments, the bees wished to return to their hive, but a great number (young, with memory but little established and effaced by the swarming), no longer knowing how to distinguish it in space, flew towards all those of the other hives which were painted blue, and towards them alone. They were badly received there and their corpses strewed the earth, but only under the doors of the hives painted blue.

The bee which goes into a room where it smells honey only ventures cautiously. Von Buttel having a honeycomb for experimental purposes at the further end of his laboratory was very astonished, after having opened the window, to see bees enter confidently and fly quite straight to it. He concluded therefrom that they must already know some room or other. But the riddle was explained. At twenty paces away a bee-keeper had several hives at the end of a garret, and these were his bees, already familiarised with the darkness of a room, which flew so surely into von Buttel's laboratory. Similarly, plundering bees, recognisable by their shabby chitin, are at first prudent and fearful when they begin their business. But the success of their incursions makes them more and more audacious and insolent. They even get to the pitch of intimidating and hypnotising the bees of the hives they pillage to the point of making them disgorge honey. It is certain that bees learn.

A hive in which the population is weakened, sees also the weakening of the force of instinct of its bees. They cease to defend themselves against their enemies (moths and robber bees), become neglectful and lazy, and no longer defend their door. When the queen remains alone with several workers, the latter even cease to get in the honey which is put before them. It is complete discouragement, final despair. These reactions vary with the varieties of bees.

Von Buttel points out further that the manner and gait of bees enables them to be better distinguished as friends or enemies by the guardians of the door than their odour. Indeed, when a robber new to the game tries to enter into a strange hive by prudently examining it, it is often attacked in the air, before it has even set foot there. Here the sense of smell cannot be in play. On the contrary the expert old robber which flies at once to the hive, without hesitating, straight by the door, is scarcely molested. Similarly the swarms which have lost their queen and which enter with confidence buzzing joyfully into a strange hive are nearly always well received there, thanks to their behaviour. Finally, bees which have been narcotised, having forgotten their hive, enter with confidence, without hesitating, into a strange hive, and are nearly always well received there, probably for the same reason.

Von Buttel refutes the opinion of Müllenhoff, who supposes that the shape of the body of bees depends on that of the cell in which they were developed. On the contrary he accepts with certain restrictions that by which Müllenhoff attributes the regular polygonal form of the cells of the comb not to the art of the bees, but to a pure mechanical effect of compression of the wax. I may be permitted to ask at this juncture if Müllenhoff thinks he can explain by the same mechanism the regular polygonal form of the cells which wasps construct in paper?

Von Buttel draws attention to certain games played by bees belonging to well-stocked strong hives on beautiful evenings. Rows of bees swing in rhythm, head downwards, making a kind of rustling. Bee-keepers say that the bees swing or "plane."[1]

Finally, von Buttel does not trouble to refute the very superficial opinions of de Wundt (*Vorles. über die Menschen und Thierseele*, 1863), opinions based in great part on erroneous or incomplete observations. Moreover de Wundt himself abandoned them later.

Memory of Time and Association of Memories in Bees[2]

I have clearly and irrefutably proved by experiment the existence of memory of localities in the social insects, especially among bees, and I have shown no less clearly that in the latter insects the sense of smell is very badly developed. They are unable to detect honey, even at a few centimetres, when no visual indication nor any memory makes them suspect its existence. A casual observation made recently has afforded me clear proof that bees possess the memory of time.

For several years we have taken our meals during the summer in the open air on the terrace. In the morning, from 7.30 to 9.30 or 10.0, preserves are provided, which remain upon the table, for, the children going to school at an early hour and the elders rising late, breakfast is a movable feast. At the midday repast there is nothing sweet on the table, or, at the most, a sweet dish at dessert, which is quickly disposed of. In the afternoon, at 4.0, preserves reappear for half or three-quarters of an hour or more.

A hive of bees, which served for my experiments in 1901, and which was then situated 90 to 95 paces from our table, was moved during the last year (1905), and now stands 120 paces from it, being thus farther off by a quarter.

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[1] "Raboter."

[2] *Comptes rendus de l'Association Française pour l'avancement des Sciences; Congrès de Lyon*, 1906.

The bees never came to eat the preserves on our table in previous years, nor this year, although they visited the surrounding flowers in the garden and on the terrace in great numbers. But, on June 17th, 1905, the neighbouring farmer's wife cooked some cherries and placed them at her window, which is surrounded by flowers and situated between our table and the actual place of the hive. A bee must have discovered these cherries by accident, for, several hours later, a whole swarm of these insects descended upon them. From that time the bees transferred their attention to the windows and other structures. They ended by discovering preserves on a window opening upon our terrace. Several days later, one of them found those which were upon our table and returned to them several times. Then it was followed next day by one or two companions. In this we have the phenomena—although elementary—of instinctive reasoning by analogy.

Relying upon my old experiments, I predicted that soon a whole swarm would burst upon the table and make breakfast impossible. Indeed the number of bees augmented rapidly. They pitched upon the cups and plates, searching everywhere for preserves, with which, when found, they gorged themselves.

But, and this is the remarkable fact, after ferreting about all over the table for a day or two at midday and finding nothing, they entirely ceased to appear at that hour, and came only in the morning from about 7.30 to 10.0 to take the breakfast preserves and between 4.0 and 5.0 in less numbers. On July 17th, such a swarm of them came in the morning that we were obliged to abandon the meal, taking refuge elsewhere and carrying away the preserves. I would emphasise the fact that preserves remain much longer on the table in the morning than in the afternoon.

At midday not a bee appeared. At 4.0 they came in moderate numbers and we could take tea and preserves without being too much worried.

I then gave the formal order to put the table as usual on the terrace next day, July 18th, but not to put any preserves thereon. This was done. About 7.30 I watched the table and saw a large number of bees visiting it. I went to breakfast about 8.0, and I observed that numerous bees, some twelve, fifteen, or more at a time, flew all about, alighting upon the cups, plates, loaf of bread, saucers, butter, coffee-pot, and milk-jug, searching vainly in every direction, with great perseverance. They examined every receptacle more or less resembling those in which they had found preserves the day before at the same time. Ten o'clock past, they ceased to come, and, at the midday meal, one single bee came flying for an instant towards the table. At 4.0 one or two returned to fly round the table, but without persisting. On the morning of the 19th, from 7.30 to 9-30, a certain number still returned, but much fewer. They alighted very rarely on the table equipage and did not remain there long. At midday more bees returned than on the preceding day, as if the absence of the morning honey had impelled them to search at another time. They also came back at 4.0, and, on giving them preserves, some brought back others. On the 20th, from 8.0 to 10.0, the same condition of things occurred as on the 19th. I placed some red geranium leaves upon a plate, but they paid them no attention. I plastered a large spot of jam on the inside of a drinking-glass and placed the glass turned up on the table. Many bees flew close to the glass, to the place where they saw the spot of jam, but always flew off, smelling nothing but the glass at their approach. None settled at the base, near the opening of the glass close to the table, *i.e.* to the only place whence they could have been able to perceive the smell of the jam. At 10.0 all had disappeared.

These facts clearly prove that bees possess not only the memory of places, but also that of time. Indeed, they returned to the same place and examined the objects, or analogous objects, *only at the times at which they had previously found preserves there*, and, after several disappointments, only once at midday, at a time when they had found nothing. It may be added that the temperature was agreeable, so that it was not the too great heat of midday that prevented them from coming.

Nothing could be more amusing than to see the bees examine in every direction the empty cups and plates, white as well as blue. They went, however, a little more often to the latter, blue being, according to Lubbock and H. Müller, the colour they prefer. It goes without saying that only the regular intermission of the placing of preserves on the table permitted the attainment of this result. In my previous experiments I was content to place honey on certain formed objects, arranged and coloured differently, to demonstrate the faculty of orientation in space in these insects according to direction and colour, as Lubbock did, but with more precision.

Several additional observations have yet to be noted.

At first the bees mistook the sugar, of which they did not recognise the sweet taste on account of the dryness of the lumps. But by dint of ferreting about, a certain individual ended by discovering, by the extension of its proboscis on the sugar, the taste of the latter, and that by moistening it a little with its proboscis (did it disgorge some of the contents of the stomach? I was unable to detect it), it obtained something sweet. Briefly, the trick was done, and the bees invaded the sugar-basin, licking the lumps of sugar, so much so that we had finally to cover it.

My wife, from sympathy with the bees, beginning to give them sweetened water and jam, after several days they ceased to come only at the times of certain meals, and in this regard the experiment was spoiled. But this taught them better and better to discern the objects and the circumstances which permitted of their finding the preserves, sugar, and cakes. They still rapidly examined every new object placed upon the table, and especially everyone coming to sit at it, but rapidly, and without stopping, where they found nothing. The pot of jam even was abandoned so soon as it was covered with a saucer. On the other hand, whenever a spoon or plate showing traces of jam was found by a bee which settled and remained there, a whole swarm followed after a few minutes.

It was no longer any use to place the table some yards away, under the verandah, for the bees quickly followed us there.

This fact apparently contradicts the observations of Bethe, according to whom bees whose hive was suddenly displaced returned, not to the hive moved only some yards, but to the exact spot in the air where the entrance previously was.

As a matter of fact, as von Buttel Reepen and I have already proved, it is not the fact, but the theory of Bethe that is contradicted. In Bethe's case the bees were drawn to a single point in space—the entrance of the hive; and this had become absolutely mechanical by long habit. They flew to it without reflecting, without searching, guided by their strong sense of aerial topography (*vide supra*). In our case, on the contrary, we made various experiments, in the course of a few days, as much with the time as with the different and differently placed objects on which we placed the preserves. This is the reason the bees in our case exercised their faculty of discernment and of varied associations, that is to say, their small plastic faculties, before a single habit became automatised.

However, von Buttel has proved that displacement of the hive only deceives bees for quite a short time, for they soon discover its new position and make for it.

Our bees became thus better and better practised and could rapidly discover anywhere each little spot of preserve and distinguish it from other spots, such as those of coffee, butter, etc. Nevertheless they often examined these latter for an instant.

All who observed this with me have been able to verify the gradual change two or three weeks produced in the way the bees behaved, that is to say, the effect of the exercise and the progress of their discernment in searching for and discovering preserves, not by smell, but by the association of visual memories.

However, von Buttel Reepen[1] has made one observation by which the memory of time has already been proved in bees. He noted that buckwheat yields honey only in the morning, and that, owing to this fact, bees habitually plunder this plant before 10 A.M., whilst they plunder others all day.

What makes bees particularly suited to the demonstration of the point in question is their bad olfactive faculty, which prevents them from directly recognising the smell of honey, preserves, etc., at more than a centimetre distant. They are guided by visual memory combined with gustatory memory, and conduct their researches by the aid of an instinctive reasoning by analogy. From the moment they have found something the taste (sweet) of which pleases them, on any object and at any time, they return to it and thoroughly examine objects of similar aspect in the neighbourhood and even elsewhere. They repeat the examinations for a certain period—*but they stop them soon, then and there when they find nothing*—to concentrate their attention upon the objects where and the times when they find what they seek. The visual memory of colours and forms enables them to retrace their way and to distinguish the object which encloses the sweet material which they have found and analogous objects. Taste fixes for them (by the desire) the visual memory of the object which encloses something sweet. The sense of smell enables them to distinguish at a very short distance (1 cm.) the sweet or honeyed object from that which is not so or is no longer so.

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[1] *Biolog. Centralblatt*, 1900.

As long as the object found continues to enclose the sweet substance the bee returns to it without interruption at all hours of the day, and is followed there more and more by its companions, especially if it is not too far from the hive. But if the presence of the sweet material on the object is subject to a *regular diurnal periodicity*, the bee, not finding what it seeks at other times, concentrates its visits on the moment of the day at which its memory recalls to it that it has always found something. Thus, it has memory of time, that is to say, it associates its visual and gustatory impressions in sequence, similarly to bearings in space, or coexistence, just as we do.

Wasps (*Vespa germanica*), which have the sense of smell at a distance well developed in their antennæ, lend themselves very badly to this kind of experiment, for they discover at a distance what they seek by direct olfactory perception. Only wasps with severed antennæ behave like bees. I recommend the above observations to Professor Plateau, of Gand.

Comparative Psychology is an as yet almost unexplored territory and but little understood, for want of approaching it by the best side, that is to say, by carefully made observations. It is involved either in metaphysical dogmas, like those of Bethe and others, or in shallow anthropomorphism which confounds inherited instinct and its automatisms with the plastic judgment of the individual, based upon memory and association of memories or sensory impressions.

Why then are so many modern men of science still so stubborn as to refuse to comparative psychology its position, even at a period when histology demonstrates more and more the complete unity of structure of the nervous system throughout the animal kingdom, including man, whilst psychophysiology proves with increasing clearness that every human psychological or introspective phenomenon is nothing of itself, but merely the internal reflex of a nervous or neurochemical activity of our brain?

Let us be thoroughly imbued with the truth that each species and even each polymorphic animal form has its special psychology, which should be specially studied and which depends, on the one hand, upon the development of its muscles and senses, and, on the other, upon that of its brain.

CHAPTER XII

JUDGMENT, MIND, AND REFLEXES

Is Comparative Psychology allowable? Does it exist?

OUR studies on the senses of insects have brought us into the midst of the province of the mind of the insect, especially of the social insect. But we are stopped at the most convenient moment by the recent works of several German authors, Bethe, Beer, Uexküll, and Loeb, among others, who, in the name of the exact sciences, have disputed the possibility of a comparative psychology. In their opinion, everything must begin again; we have so far only been anthropomorphic. We have not any right to admit either sensations, perceptions, or memories in animals. We only observe in them reflexes more or less combined when they constitute instincts. It is necessary to remodel all the nomenclature, which is rotten with anthropomorphism. One will no longer be able to speak of vision, nor of smell, etc., among the beasts, but only of photoreflex or chemoreflex. The odour of the nest will be the substance of the nest, the combined individual, family, and reginal odour of the nest of bees will be consequently the substance of the individuo-regino-familio-nido-chemical reflex. What we have thought we have recognised as memories and associations will be the unknown forces A, B, C, D, etc. In this manner one may be able doubtless to arrive at exact formulæ (mathematical? chemical?) of animal life, and our biological works will appear to our successors like the alchemy of past centuries to the chemists of the nineteenth.

It must be confessed that the programme is imposing. At one blow, scattering all doubts to the wind, it cuts a way through the tangled forest of inductions, full of poetry and beauty, which had been called, until the advent of Bethe and his colleagues, natural science, and gives us a mathematical exactitude which is rather dry, it is true, but enables us to calculate everything without a mistake, from the cubic content of a room to the distance of the fixed stars. It is so imposing that it is too beautiful, and M. Bethe himself, the partisan of perfect exactitude in theory, at any rate, will allow us to pass his views through the crucible of criticism.

Let us state in the first place that Bethe has already been criticised by Wasmann and by von Buttel Reepen. We have just analysed the criticism of the latter.

Wasmann (*Die psychischen Fähigkeiten der Ameisen;* Stuttgart, 1899, Verlag v. Erw. Naegele) has submitted Bethe's work to a masterly criticism to which we shall return. We cannot here analyse it in detail, because it goes beyond our limits of the senses.[1] I refer to the fourth part of this work

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[1] Several important facts must be noted nevertheless. Bethe thought he proved that ants only recognised themselves by a "nest or family substance." He had bathed certain species (*Camponotus*) in a broth made with the bodies of a hostile species (*Tetramorium coespitum*), and had found that after that the *Tetramorium* ceased to attack the *Camponotus* and treated them as friends. Wasmann has remade the experiment several times, varying it in different ways, but instead of confirming Bethe, he has found that the bathed ants are attacked and killed, *i.e.* that the enemy recognised their hostile odour beneath the guise of the friendly odour in a very short time. At the most there is at the commencement several instants of indifference.

Wasmann refutes with care an assertion of Bethe, which is so absurd and so contrary to every fact of observation, that I have not even taken it up. Bethe thought he had proved by the aid of a superficial observation that "*the track which goes, for example, from a tree to a nest cannot assist an ant to go from the nest to the tree, and that the track which goes from the nest to the tree cannot help an ant to return to the nest.*" If Bethe knew the habits of *Formica* and *Polyergus* he would have been afraid to have committed such an enormity, seeing that these insects orient themselves, one may say constantly, on the return by their outward track (in the sense of the topochemical sense of smell). As Wasmann says very well, the return of an army of *Polyergus rufescens* and the removals of *Formica* would be impossible if Bethe was right. Wasmann pays attention to the "form" of the odorous track, as a means by which the ant distinguishes the outward track from the return track. That corresponds partly to my theory of the topochemical sense of smell. Further, Wasmann shows by experiments controlling those of Bethe the error of his conclusions, and insists, like myself, on the fault which Bethe commits in applying to ants in general the manner in which *Lasius* orient themselves. He concludes that it is by associated memories that *Polyergus* can find their way again even after several weeks.

Wasmann rightly points out that *Formica* know so well the immediate surroundings of their nest that even the removal of a surface of earth with a shovel does not disorient them. I refer to what I have said above against Fabre in regard to *Polyergus*. Here the general direction and vision suffice. They are too sure of their fact; the memory of known places gives them this sureness, as Wasmann has pointed out.

(Albrecht Bethe). Wasmann himself, starting from the point of view of a Jesuit father, nevertheless shows how to preserve a remarkable scientific objectivity for all that does not touch man. He refutes Bethe, especially with the help of already published experiments (his own, Lubbock's, Janet's, mine, etc.), with crushing logic for Bethe. But it is on the other hand necessary to study the fundamental ideas of the criticism of Wasmann, because this author falls into another danger due to his religious dualism.

WASMANN, *l.c.*

As a dualist by religion, Wasmann begins by admitting Bethe to be right where he attacks the "*panpsychism of Haeckel.*" Let us begin by making ourselves clear on this point. The panpsychism of Haeckel, like the polypsychism of Durand de Gros (Haeckel, *die Welträthsel*, 1899; Durand de Gros, *Electrodynamism vital*, 1855, and *Essais de physiologie psychologique*, 1866, Paris, Baillière) is in the main nothing but the monism of Giordano Bruno, of Spinoza, and others, metaphysical monism, to which we shall return. Haeckel is, further, not consistent in the way in which he develops it, and gives thereby an easy handle to criticism.[1] I will, give further, on my opinion on the subject, and this opinion will be at the same time the refutation of Bethe and Wasmann on this point.

Bethe calls "*Modificationsvermögen*" (faculty of modification)

Wasmann gives some pretty proofs of the vision of *Formica* and of the relation of the vision of ants with the mimeticism of ant-loving insects. He shows clearly the faculty of communication (false language) of ants, as I have done in my *Fourmis de la Suisse*, and as von Buttel has done for bees, adding thereto numerous facts. He admits, as I, that it is a question of very varied signals, of which the comprehension is fixed by instinct, as is their execution. He gives a very complete catalogue.

Finally I recall here my own experiments, vi. 3, vi. 4, vi. 5, vi. 6, and v. 2 of my *Fourmis de la Suisse*. These show therefrom that the ant remembers both good treatment and bad treatment which it uses towards another or which it receives from another. Its friendships and its enmities, its sympathies and its hates are strongly influenced thereby, and such fortuitous facts can triumph over the instinctive antipathies and sympathies of odours, *i.e.* the family chemoreflexes of Bethe.

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[1] I cannot completely agree with M. Forel upon this matter. From a perusal of what follows later he appears to me more in accord with Haeckel than the above sentence would lead one to think. In regard to the criticisms upon Haeckel, I would recommend to the reader the study of M'Cabe's "Haeckel's Critics Answered," published by the Rationalist Press Association.—TRANS.

what I have called plastic activity of the nerve centres, in contradistinction to their reflex or automatic activity. It is to him (and there I agree with him) the condition of the faculty of experience or of individual apprenticeship. But all that which is not thus learned is *reflex* to him. Wasmann points out to him that between the two there is the whole domain of instinct, that is to say, of hereditary nerve actions and reactions co-ordinated in a complex manner in course of time, to accomplish complex ends. At all that Bethe turns up his nose; it is scratched out by a dash of his pen and thrown into the bag of the big word "reflex."

In the second place, Bethe puts into his second bag (there are two for him, and only two) all that he calls "*psychische Qualitäten*" (mentality), and defines it by his "faculty of modification." The term is bad, for instinct can also modify itself; I prefer the term plastic or individually adaptable cerebral activity. This "*mentality*" he refuses to insects, basing himself onexperiments as superficial as they are badly interpreted, experiments which show from first to last that Bethe has very little knowledge of the insects of which he speaks. We have, we believe, sufficiently proved this in what has gone before. Those who have not yet been edified in this matter have only to read the work of Wasmann and my *Fourmis de la Suisse* (Geneva, 1874: Nouv. Mémoire de la Soc. Helvet. des Sci. Nat.).

It must be admitted, therefore, that insects are capable of perceiving, of learning, of recollecting, of associating their recollections and of utilising them to accomplish their ends. They have various emotions and their will is not purely instinctive, but offers individual plastic modifications, adapted to circumstances. Here we are plainly in agreement with Wasmann, who brings a pitiless logic to the demonstration of the fact. It is indeed *piquant* to see the dualism of Bethe thus undermined by a Jesuit father. Indeed, Bethe sanctifies his dualism by making mentality hatch the "conscience," like a *deus ex machina*, among the vertebrates.

But my learned and honourable friend, M. Wasmann, will allow me to tell him that if the dualistic knife of Bethe is wrong in cutting off the soul from the brain of invertebrates, it does not follow therefrom that the dualist knife of the Jesuit father will be right in separating it a little higher up, between man and his brain, and refusing it to the higher vertebrate. A few explanatory words are necessary on this subject.

Let it be stated first that Bethe is mistaken in establishing a hard and fast separation between plastic and automatic activities (his "reflex" and his "faculty of modification"). The gradual passage of the conscious plastic activities of man to the secondary automatic activities or habits, gives us the daily example of all the transitions possible between these two terms, of which, Bethe following Descartes arbitrarily makes antitheses. But inherited instincts themselves are more or less fixed and automatic, offering thereby transitions to plastic activity, and thus it is the same for simple reflexes. They are more or less inhibited and modifiable, according to the case, by plastic or "voluntary" activities, which combine with them to every degree.

After having supposed that everything was reflex among ants, Bethe says that dogs and monkeys are compelled to *learn everything*, even to walk and to eat, like man. Here Bethe (and to some extent also Wasmann) makes a charming confusion. Let us endeavour to explain it simply and in a few words from the very first by two examples. The new-born rabbit can scarcely drag itself along and has its eyes shut; the guinea-pig, on the contrary, runs with agility from the time of its birth. Therefore, according to Bethe, the rabbit will have to "learn," the guinea-pig not. Notwithstanding, this is neither probable, nor even certain.

The reason of these apparently contradictory facts is that the rabbit is born at a stage much more embryonic than the guinea-pig; its brain is still more grey, the nerve fibres are too little myelinated to be functional. This simple fact shows that Bethe wrote without reflecting. Many nervous activities appear at a certain age of themselves, by embryogenic cause, and then we imagine, like Bethe, that they are "learned." But this is *also the case with man*, and we think we teach our children a crowd of things which they learn by themselves. Further, the "mamma" also helps the little monkeys and even the little dogs in their first attempts at various acts. Wasmann himself remembered that the apprenticeship to walking in the human child is in large part only the exercise of reflexes; he might say entirely. But we will add that in *all* the human and animal activities there is an hereditary element which is called *predisposition*. And if one takes the trouble to analyse the facts closely, one finds that between an instinct inherited complete, having no need of apprenticeship, and the highest act of the plastic human intelligence, there is an uninterrupted series of transitions. It is here that I begin to leave Wasmann. In reality, the human child is born with a brain almost wholly grey, embryonic to the highest degree, scarcely functional; the spinal marrow and the ganglia of the base alone have their reflex and automatic apparatus sufficiently myelinated to be capable of function. But in man these lower apparatus are very largely dependent upon the great brain which dissociates their functional activity, relatively independent in the other mammals, by means of the psycho-motor pyramidal tract. That is why the new-born infant is so inept and so dependent. It is only by becoming myelinated during the first year of life that its brain becomes capable, little by little, of receiving the impressions of the senses and of putting, little by little, its muscles into play, not directly, but by playing on the reflex spinal and other centres by means of the enormous cortico-medullary pyramidal tract. Further, in the ascending series of mammals, the relative dependence of the medullary, bulbar, and other centres on the great brain augments with the relative volume of the latter and of the pyramidal tract.

The old scholastic philosophy did not know the human brain. Starting from a psychology, badly understood for want of knowing its organic foundation, and from metaphysical speculations, it founded axioms and entities which do not really exist. But one knows that the words representing our abstractions, false or true, or partly false and partly true, have a constant tendency to become materialised in our mind and to replace there, not merely in form, but in reality, the ideas which they represent. This is the great weakness of the human mind, the opposite of the advantages which abstractions of language and written encyclopædias of our knowledge present. Language and books are crammed with words which are taken for things. We end by attributing reality to them.

It is upon the horn of this dilemma that Wasmann impales himself. He allows to the higher mammal and to the insect the faculty of sensory perception, that of apprenticeship, of imitation, of emotions, etc. We absolutely agree with him on all these points. But he refuses them *intelligence*. But how does he define it?

Man, says he, has an *intelligent intention. He is capable of drawing conclusions about new relations from past experiences.* This is the definition which Wasmann gives of human intelligence. He divides the faculty of learning or of knowing individually into six heads, which he sums up under two chief classes:—

I. *Knowledge acquired spontaneously*—

1. By the instinctive exercise of the congenital reflex mechanisms, which are put in play by the muscular sensations of the animal.

2. By the experience of the senses, which form, *by their proper activity*, new associations of sensations and representations (sensory memory).

3. By the experiences of the senses and *the intelligent conclusions from old relations to new relations* (sensory memory and *true intelligence*).

II. *Knowledge acquired by foreign influences*—

4. By the evocation of the instinct of imitation by means of example.

5. By training, by means of which man inculcates in other beings endowed with sensations, new sensory and representative associations according to his intelligent plans.

6. By intelligent instruction, by which an intelligent being learns from another intelligent being not only to form spontaneously new associations of representations, but again to draw new conclusions from his former knowledge.

Wasmann assigns to man alone his six categories, and to him exclusively categories I. 3 and II. 6. To animals he allows, according to their development, the categories I. 1 only, or I. 1 + II. 4, or I. 1 + II. 4 + I. 3 + II. 5. Nevertheless he does not presume to guarantee I. 1 to protozoa. His category II. 5 naturally supposes an intelligent master.

The first criticism that I have to make on these categories is that in Nature no such distinct categories exist. Wasmann divides where there is no division. They evolve from one to the other, both in the life of the individual and in that of the species. The human embryo begins by being like a protozoan, and from the protozoan it rises gradually to the man by the phylogenetic chain. Wasmann, therefore, errs fundamentally by starting from decided categories to establish therefrom absolute differences which do not exist.

He allows that in the higher animals one obtains by training very considerable intelligent effects which one cannot obtain in the insect (ant, etc.). He is absolutely obliged to allow it, for he would be much embarrassed to teach an ant or a wasp what one teaches a monkey or a dog. But that is where he makes a mistake, this is apropos of his category I. 2. He depreciates too much this faculty of development and of individual experience in the higher mammals. Still too impregnated with Cartesianism, he only sees in the effect of their training the human intelligence which echoes there (like Netter, for example), and does not take at all sufficient account of the spontaneous experiments which the higher animals (with which he is not occupied) make for themselves.

The experiments of von Buttel Reepen (also my own with the dahlias apropos of Plateau) on bees have especially shown us the *rapidity* with which insects learn in the direction of their inherited instincts. But one must not forget all at once, as Wasmann does, their "*frightful stupidity*" for everything which is not adapted to their instincts, a stupidity so admirably described by Fabre, whose description approaches caricature. Vertebrates with a developed brain are not guilty of such stupidity, because they "understand" much better and are much more capable of profiting by their experiences, combining their recollections and getting over difficulties. I need only cite the dog, that everybody knows. When one goes a little into the habits of wild vertebrates, one discovers that they are much more apt to make personal experiments and able to profit by them than is supposed by those who do not know them. Every hunter knows this, and I appeal therein to everyone who knows vertebrates. S.A.R. Princess Thérèse of

Bavaria, in her remarkable book (Thérèse Prinzessin von Bayern, *Meiner Reise in den brasilianischen Tropen*; Berlin, 1897, Verlag von Dietrich Reimer, S. 495 *u.ff.*) on her voyage to Brazil, shows without any bias, and in a very objective manner, the character of a coati (*Nasua socialis* Wied) that she watched for four years. I recommend such psychological studies on the vertebrates to everyone. The author, to whom no one can attribute a want of objectivity, points out with great justice that in shutting up animals (I add also in training them too much) one hinders their natural intelligence from developing and from revealing itself (just as in man!). Princess Thérèse allowed her coati complete freedom, and this is what adds to the value of the observations made on the astonishing memory, distinctions of persons, sympathies and various actions of this curious animal.

I refer, moreover, to Romanes (The Intelligence of Animals), and to the remark that I have made in the sixth edition of *Gehirn und Seele* (Forel, *Gehirn und Seele*, 1889, Verlag v. Emil Strauss, p. 34 *et seq.*).

It is impossible for me to treat in the present work on the cerebral physiology of human psychology. What I affirm is, that the deepening of this study shows in an indubitable manner that it is only the evolutionary expansion of animal psychology, an expansion grafted on a fundamental fact, or, rather, on the historical sequence of two fundamental facts: oral tradition and written records. These two facts are the result of oral language and of written (and later printed) language, which are themselves the consequence of a progressive cerebral development of which we find every root and every beginning in the higher animals. If we could restore to life and observe *Pithecanthropus erectus* with his cranial capacity (calvarium) of 570 c.cm., and Neanderthal man (920 c.cm.), we should have before us the evolution of language. Modern man has a cranial (calvarium) capacity of about 1100 to 1300 c.cm., whilst the great anthropoid apes have only about 280 to 290.

In 1877, at the time of my "qualification" as Privat-docent at the University of Munich, I stated as 7th thesis, "*Sämmtliche Eigenschaften der menschlichen Seele können aus Eigenschaften der Seele höhrer Thiere abgeleitet werden.*" (One may derive all the faculties of the human mind from the faculties of the mind of the higher animals.) I have not one iota to retract to-day of this thesis. I shall allow myself to develop shortly two questions which belong to it in two magazine articles: "*Die Factoren des Ich*" in the German journal *Die Zukunft* of Max Harden, and "*Perfectibility*" in the American journal *International Monthly* (Macmillan & Co., New York). I refer the reader to them. In the latter of these articles I show how the human perfectibility arises from the animal or evolutive perfectibility by two steps—the perfectibility by oral tradition and the perfectibility by written records.

It is not difficult to see that our dualists always make a forced comparison between animal routine and the most developed faculties of higher men, faculties which are all grafted on written record, and thus allow of our brain being utilised in an unheard-of manner. Perched on the shoulders of our predecessors by means of this record, we are too much inclined to overdo ourselves. Indeed, we can already find the animal roots of our higher faculties, if we compare with animals, not Socrates or Goethe and what we know of them, but an illiterate of the Aryan race (of our race) and a learned man of inferior race. The first has in his brain the necessary hereditary energies to become superior by instruction, but they are not developed. It is the untrained monkey or dog compared with the well-trained monkey or dog. The learned Veddah or Bushman appears to the superficial observer much superior to the Aryan illiterate. But this judgment is false. Even the negro, if closely studied, approaches much to category II. 5 of Wasmann. Indeed, he keeps what he has obtained by training (his instruction resembles an animal's training even more closely than the parrot teaching of our school) only so long as he remains in contact with the white. Left to himself, he rapidly deteriorates, and is especially incapable of transmitting civilisation to his descendants (see Hayti and Liberia, negro colonies which have been founded by using only negroes of especially intelligent races). He only possesses the categories I. 3 and II. 6 of Wasmann to a limited degree, very inferior to ours. And on the other hand I contest the exactness of the assertion of Wasmann, who absolutely refuses his category I. 3, for example, to the higher apes and to dogs. Doubtless it is extremely rudimentary in these animals relatively even to that of the most inferior human races. This is not astonishing, if we compare the human brain to theirs! But it exists. The dog that loves his master, and even patiently allows him to perform a surgical operation (I have done so myself), whilst it mistrusts a stranger, and especially one who has done it harm, or has shown it antipathy, this dog, I say, proves thereby that it deduces from old experiences to new relations. It foresees what will happen if it does such and such a thing. Doubtless, in comparison to our power of foresight and resolution, this can hardly be called complicated. The dog further cannot explain its mental processes to us by a language of which its brain is not capable, for want of sufficiently developed convolutions, but the element is really there. Bethe and Wasmann are opposed in this sense, that the former exaggerates the relation between the mind of the higher mammal and that of man, and draws an absolute line between such a mind and that of the insect; whilst Wasmann, on the contrary, exaggerates the relationship between the mind of the insect and that of the higher mammal, in order to separate this latter from that of man by his artificial definition of intelligence. The truth lies midway, but the mind of the insect differs from that of the mammal especially in quality, as much on account of the qualitative differences of the senses, differences which we have analysed, as of the peculiarities of the instincts of the articulates in general; these instincts are very complex, and are combined with a faculty which serves a very short apprenticeship to memory, whilst the plastic adaptability in every direction other than that of specific instinct is extremely limited in these animals. In the mammal, on the other hand, plastic adaptability is infinitely superior, and the instincts are much more simple. This makes comparison more difficult. Between man and the higher mammal, especially the anthropoid ape, the difference is above all quantitative. And even though the brain of an uncultured savage of inferior race comes infinitely nearer to ours than that of the highest living ape,[1] his manners and his intellectual horizon are in large part more akin to those of the Orang-outang than to those of a distinguished and cultivated man. Many of the citizens of our towns and villages live a life and think in a way more like that of the brute than that of the man "of head and heart." These facts are connected with the education or the non-education of the brain by the help of records. But if one puts aside all bias and all prejudice, one will find therein precisely the confirmation of the evolutionist and monistic opinion in everything which concerns the cerebral domain. Only, to find this confirmation, a profound study of the human brain and of its normal and pathological functions is absolutely necessary. The study of psychiatry, of limited responsibility, of criminal anthropology, of pedagogy, of hypnotic suggestion, of physiological psychology, of sociological laws, and of the ethnology of the human races, is necessary to the comprehension of so complex a subject. But the more deeply one goes into it, the more apparent is the intimate relation between the human mind and that of its closest animal neighbours, if one does not intentionally cut off the horizon from view by an artificial limit, and an impermeable screen.

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[1] "The cerebral differences of man and ape are not of more than generic value."—Huxley ("Man's Place in Nature").—TRANS.

It must not be forgotten that abstract thinking is scarcely possible but by means of a conventional language. If there is a well-marked difference between man and the higher mammal, it resides in language and in the faculty of abstractions, and not in that of deducing something new from an old experience. But we find the rudiments of language in the higher mammal and a rudimentary language in the inferior man. The dog and the monkey have, without any doubt, the general representations which form the primordial basis of abstract ideas.

If monism postulated for the lower animals complex qualities, of which the existence is neither demonstrated nor probable, one would plainly be right in reproaching it for doing so. But monism makes no such demands. It is content with stating the evolution which makes the complex derived from the simple, and refuses to cut limits which do not exist. If it attributes introspective reflection, or consciousness, to simple phenomena by reason of analogy, it is because it defines the term consciousness quite differently from dualism. To the monist this is in no way complex and has nothing to do with "knowledge," it is a simple introspective aspect of every being.

Finally, recognising that it is absurd to grant to the mind the notion of energy, while separating it from the brain (because then one rematerialises it and reduces it to another form of energy, which puts afresh the peremptory question of monism—see below), Wasmann denies its possession. For him the mind is "quite another thing," something absolutely independent of the notion of energy and of the law of its conservation. But, then, how is a reciprocal action of the mind on the body and of the body on the mind possible without loss or increase of energy, without which we should see causes without effects and effects without causes, action without reaction, or vice versâ, which we do not see? To this Wasmann replies, "But we do see this, in miracles!" In *Stimmen aus Maria Laach*, Freiburg i. B., 1900, Heft 2: "*Ein plötzliche Heilung aus neuester Zeit*," he describes to us the sudden cure of an old fracture, complicated with pseudarthrosis, by the Virgin of Lourdes, a cure duly verified by doctors and witnesses. He even figures the reunited bones of the patient (Peter de Rudder). Here, according to him, the personal Creator shows that He is above natural laws by occasionally giving them a shock!

My excellent friend M. Wasmann will excuse me from following him on such delicate ground as that of miracles. The "proofs" which he gives of the miracles of Rudder have not convinced me in the least. Up to now all "miracles" have vanished, that is to say, have been explained little by little before the torch of science, and we have every reason to believe that it will be the same in the future.

After having refuted the deductions that Bethe draws from his experiments in order to reach a kind of mechanical comparative psychology, and those which Wasmann draws from his experiments in order to reach a dualism between the human mind which he considers independent of the law of the conservation of energy, and that of the animal, it remains for us to examine the real difficulty of the question, which we shall do in several chapters as briefly as possible.

ALBRECHT BETHE[1] *Mechanism and Exact Science in Physiology and Psychology. Terminology of Comparative Psychology*

Bethe vaunts the exactness of physiology and accuses Wasmann and us of dealing in anthropomorphism and subjectivism. Let us see a little what his exactness and his terminology are worth.

There is only one exact science: mathematics. But mathematics are only exact because all their truths are tantamount to equations.

If I say $2\times 2=4$; or $V=\pi h\left(\frac{2d+d^1}{6}\right)^2$; or lastly, $25=25$; or if the reader prefers, M. de Lapalisse was still alive a quarter of an hour before his death, which is tantamount to saying, Being still alive he was still alive or to be alive = to be alive; from the point of view of logic it comes to the same thing. Mathematical or absolutely exact truths are . . . another way of saying the same thing. They only serve to explain complicated equalities by means of abstractions represented by signs. They therefore only assume as proved, or rather pay no heed to, the intrinsic value of terms.

If I say $2+2=4$, or $4=4$, this is absolutely exact, because 4 is only an abstraction. But if I say 4 francs in coined silver are equal to 4 other francs in coined silver, this is no longer exact, because that supposes that a coin of a franc is absolutely equal to another coin of a franc, which is never true. We must not therefore make mathematics or exact sciences say what they do not say.

But physiology cannot even be an exact science in its calculations, because we know absolutely nothing of the physical and chemical formulæ of the life of protoplasm, which is the whole object of its studies. We know only its manifestations as far as they show themselves to us. Physiology, therefore, can only be a "natural" science, *i.e.* dependent upon observation. To wish to suppress the subjective element of every science of observation, is to desire impossibility and to lead to absurdity.

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[1] Bethe, Albrecht, *Noch einmal über die psychischen Qualitäten der Ameisen.* Pflügers Archiv. für die gesammte Physiologie, Bd. xxix. p. 39. Bonn, 1900.

It goes without saying that mathematics serve the physiologist in many chapters, and aid him to settle many problems of detail; but if the base itself be missing, the mathematic exactitude of physiology necessarily falls to the ground.

That being so, one must be terribly presumptuous to imagine oneself able "to make objective" and render exact all the terms of physiology, and especially all the terms of biology, and the comparative physiology of the nerve centres; or in other words, to think one is able to make out of comparative psychology a so-called objective mechanism of the "reflexes" of animals, and by a stroke of the pen to delete all that does not come within such limits. This mechanism assumes complete knowledge of the physical and chemical laws of protoplasmic life which we have not. And starting therefrom, it thinks it can settle by itself the most abstruse problems of biology, the complex manifestations of cerebral activity! With such feeble equipment, it further thinks it can turn up its nose at every observation which does not conform to its supposed laws, even though like that of Fechner-Weber, they be radically unsound,[1] and forbids all comparison of the acts of animals with the psychological study which we can make on ourselves, on man, a study much more fruitful than the mechanism which would reject it. It naively imagines itself able to substitute terms of mechanism for all the terms drawn from human physiology in the domain of comparative psychology. It is simply the narrowness of the specialist (*Facheinseitigkeit*). To be consistent, one must recognise that, since each man has only subjective knowledge of himself, one must disallow every "anthropomorphic," that is to say egocentric term, not only to what concerns animals, but also to all other men. Indeed, by supposing that other men have the same sensations as ourselves, we attribute to them, without exact proof, our own subjectivism. If we wish to renounce it consistently, according to Bethe we could no longer say "my wife has a headache." We should have to say: "this animal machine which I believe to be my wife makes certain facial contortions and emits certain sonorous articulations which correspond to those which I emit when I have a headache: it may therefore be possible that she may have analogous sensations to mine in like case, but I have not the right to call them headache."

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[1] Fechner was the first to recognise that his psychophysical law, which he has modestly called the law of Weber, was not a law, but merely the very imperfect attempt to find the expression of a law, where the foundations even included too much of the unknown for such a law to be just. He recognised the faults and the continual exceptions to his law. It is his rivals, especially Wundt and his school, who have exaggerated its importance.

And when M. Bethe complains that Wasmann treats him as *wissenschaftlicher Hanswurst* (scientific Jack-Pudding), I confess that I do not know what terms he ought to use to express, according to his own ideas, this supposed thought of another, in a truly mechanical and objective manner. This thought is, indeed, relative to the mind of Wasmann, which is not *his* mind, and which he does not further appear to understand. Since one has not the right to say "Odour of the nest" in speaking of the supposed olfactive sensation of ants, let M. Bethe find us the "substance," the objective term, representing the expression of "scientific Jack-Pudding" which he thinks he is able to extract from the thought of Wasmann relatively to him, Bethe! Joking aside, I for my part give up the attempt to find this term. Even in a domain less related to ours, that of the psychology of the Vedda of Ceylon, of *Pithecanthropus erectus* or simply of a dog, I defy M. Bethe to find mechanical and objective terms homologous to that of "Neststoff" (substance of the nest) to express all the biological manifestations active or passive of these beings, for example those of the emotions and of the memory of a dog. But M. Bethe, if he wishes absolutely to avoid every comparison and every term drawn from his own psychology, will be obliged to manufacture this terminology. If not, it would be Bethomorphism in the dog and even in the Vedda or in our children and our wives, who think quite differently from us, adult and cultivated men, and who understand otherwise the terms of conventional language. One can even say that no two cultivated men think the same, and absolutely comprehend in the same way the terms of their language. It is enough to read the Bethe-Wasmann polemic to be convinced of it. To be truly exact and objective, it would be necessary, therefore, to suppress all subjective things which assume that our human subjectivism exists and that it is the same in all men. It would be necessary to adapt all the terminology to this hypothesis.

M. Bethe will have to do it, therefore. But he will not be able to do it. If one wishes to replace all psychological by physiological terms, one must in reality upset all language, all history, all our culture, and rebuild them with other terms supposing the non-existence of subjectivism in others. It would be necessary for that to have two languages for everything, one for the *Ego* and the other for the *Non-ego*. M. Bethe will not succeed in that.

Certainly I am far from wishing to make apology for the humanisation of the mind of beasts. I have done, on the contrary, my utmost to combat it. But if we must everywhere insist on the differences and on the insufficiency of our terminology, that is not a reason for us to undo all comparison of the subjectivisms judged by analogy, to undermine the base of all comparative psychology. *There is no possible psychology without comparative psychology. And the physiology of the nerve centres without psychology is only a conglomerate of feet, without the head which co-ordinates them.* It is necessary, therefore, *nolens volens*, to study *psychology* and *physiology* in relation one with another, comparing their results, endeavouring to find the most exact relations possible between their ideas and the terms which are related to them, even at the risk of often falling back unintentionally into anthropomorphism. If we know this latter danger, and if we fight against it without respite, correcting it without ceasing, we shall progress, from corrected error to corrected error, slowly but surely, towards the relative truth which alone we can understand.

If, on the contrary, seeing only one side of the question, we persist in wishing to build in an instant a so-called objective mechanism where all the foundations are wanting to us for its building, we shall fall into an absurdity and arrive at nothing.

That is what I have to reply to M. Bethe and his school. In the work quoted at the head of this chapter, Bethe tries to defend himself against Wasmann, but his defence is so weak that it scarcely attempts to disguise his defeat. I therefore dispense with making the analysis. In short, Bethe is obliged to recognise a part of his errors. His defence consists especially in attacking the religious theories of Wasmann; this is best proof that he knows himself beaten on his own ground.

For my part I favour the employment of a mixed terminology, dependent on that of human psychology, but indicating as much as possible every definable difference.

Psychophysiological Identity and Parallelism (Külpe, Heymans, and the Psychologists). Monism or Dualism

The hypothesis of the Monist identity is to be preferred, in my opinion, to the hypothesis or compromise of parallelism. It is especially the term parallelism and the separation of the domains consecrated by it which I condemn, because it lends itself too much to the mistake necessary to every dualistic interpretation of facts.

At the outset let us admit that psychophysiological identity, *i.e.* that the psychological fact and the corresponding physiological fact are only two aspects of one and the same reality, is not provable by the syllogisms of the deductive method, but only by induction. On the contrary we have the right in science to presume a theory true, and to see afterwards if the facts agree with it or not. There is no necessity for us to await its syllogistic proofs. But the scientific facts of the brain and of the mind agree with the monistic hypothesis and do not agree with the dualistic hypothesis.

By identity I do not mean the identity of phenomena, but that of the reality or thing in itself which appears under two aspects, one physiological, the other psychological. Let us remember that these two aspects are subjective, like all our knowledge. But the first can be controlled and corrected by our various senses and by other persons, which is not the case (at least not directly) with the second. This is why we call the physiological aspect of nerve phenomena objective (in reality wrongly), in the same manner as the aspect of the outside world, which brings us our intelligence. This must be repeated, because one is too ready to forget it.

In an analogous way the forces which act in an electric accumulator and the matter of the accumulator are not two different realities. The protoplasmic forces which constitute the life of the cells of an apple and the apple which I see, which I taste, or which I touch, are no more than one and the same reality seen, tasted, touched, and calculated in the physical or chemical forces of its protoplasm, which represents at least four different aspects.

But these different aspects or phenomena are not parallel. When I regard or feel the accumulator and the apple as so much matter, I observe therein syntheses of energies, but not of all the energies which constitute the reality of the accumulator or of the apple. And when I analyse the combined electric forces of the accumulator or the physiology of the protoplasm of the apple I do not discover all the forces of which I have more or less recognised the mechanism. Each aspect gives me partial and symbolic knowledge of the reality. In certain cases my analysis goes a long way and is more or less approached to the complete dismemberment of the syntheses which my senses give me; in others it goes still farther. This is not a parallelism. I know that in the last place there must be identity between matter and force perceived and calculated, but I cannot reach the end for want of ability to seize all the threads.

Nevertheless there is a fundamental difference between the accumulator and the apple. In the first, I have been able myself, not to create, but at least to reassemble and adjust the forces which act, that is to say, to understand their combination. It is a machine made by me.

In the case of the apple I am not capable of this. I cannot construct living protoplasm. I can only state a part of the laws of life, such as it exists. I have not the secret of the universal power which evolves in living matter. Nevertheless, on reflection we shall see that the difference is not so great as at first appears. I have said that we do not create the forces with which we make a machine to go; we only make use of what exists or combine them and transform them. We do not, therefore, understand completely the evolution of the inanimate world more than that of the animate world.

But we can likewise in a certain measure utilise and combine the organised forces of living beings, for example, in artificial selection.

The secret which escapes us, the root of the problem, is not that of the consciousness, as we shall see, but that of natural evolution. It is the question of knowing how it comes about that the world, both in its so-called inanimate and animate parts, evolves and transforms itself little by little in a certain direction and according to certain laws, which we are merely beginning to decipher; whilst our machines, even the most admirably constructed, are absolutely incapable of evolving as we define the term, and, left to themselves, are dissolved again according to the laws of ordinary matter.

This is a point of the problem of which one cannot say beforehand that it is inaccessible to scientific investigation. On the day when man shall have found perhaps the means of making matter evolve in a certain direction without requiring to interfere perpetually himself to make his machines go, he will have made a formidable step in knowledge, which is yet far from being accomplished. We need be no longer despondent of arriving some day at a knowledge of the conditions of the formation of organic life. But if man does reach it one day, he will not have thereby made a step in the knowledge of the unfathomable and divine power, first cause of universal evolution. Indeed, being ourselves therein only a secondary machinery, we are by that very fact incapable of comprehending the divine being, the riddle of the universe, and this is what makes all metaphysical systems illusory.

The scientific error which we are attacking consists and has always consisted of dualising the phenomena of internal vision or of consciousness which reflect introspectively to our brain its own activity, and thereby the outer world which is symbolised and projected in the brain by means of the senses, making thereof a second thing, a "mind," different (parallel or not, it matters little) from cerebral energies.

To this unhappy dualistic conception, due to a play upon words, we oppose the conception of the monist identity, of which the first idea is already found in Giordano Bruno, Spinoza, Burdach, etc., a conception which alone agrees with the results since obtained by the modern science of the brain. But the ancients, who had only very vague knowledge of the brain and its functions, had made of monism a metaphysical business and had not sufficiently grasped the scientific importance of it. Spinoza, with his dogma of attributes, considered physical and psychical facts as constituting two series of different realities with different contents, but derived from one unique and monistic absolute. This is a metaphysical monism which becomes dualistic by bifurcation. This is not ours, as Heymans (see below) very well showed. We do not desire on the contrary to make a religion of it, nor a metaphysical dogma. Leaving aside the absolute which is metaphysical, that is to say unknowable, we admit identity or psychophysiological monism into the realities of the world which we know. And in admitting this identity, we unify where Spinoza divided. We do not presume to make it a religion nor a dogma. We say simply that, in admitting the said identity, the facts which appeared contradictory and irreducible agree and are explained without trouble, which speaks for the justice of the hypothesis. It is not a question, therefore, of a *word* pretending to give the *essence of the world.* The hypothesis or theory of monistic identity says simply this:

There is no mind without nerve centre nor nerve centre without mind, any more than force without matter, or matter without force. The two terms do not denote two realities, but two aspects of the same reality, of the same entity, aspects different only for the special qualitative energies of our senses, and because we only perceive them each incompletely. That being so, there exists no reciprocal action of the mind on the brain nor of the brain on the mind, any more than of the mental on the physical or of the physical on the mental. This supposed reciprocal action is merely a dualistic mistake. What have been taken for such a reciprocal action are merely the reciprocal actions of certain higher cerebral functions on the lower cerebral functions or vice versâ, actions of one portion of the nervous system upon another. And what has strengthened the mistake is the limitation of the faculty of association of conscious memories of these different inter-activities, the extent of association of our ordinary consciousness being usually more or less limited to the *maxima* of our attentional conditions.

Of the outer world we only perceive the said partial aspects (phenomena), more or less synthetic or analytic, due to the neurocymic waves[1] which it communicates to our brain by means of the sense organs. What in physiology is neurocymic wave is sensation or representation in psychology.

One sees by that that the perception of the outer world by our brain does not differ essentially from purely internal psychological phenomena. Among the latter it is merely a question of intracerebral neurocymic actions or reactions, without actual participation of the senses. That is all.

Cerebral physiology and psychology are therefore only two aspects of one part of the principle-life of our brain. What we must call consciousness is not, therefore, a special faculty of the mind which knows, but merely the whole of one of the aspects which we have pointed out: the psychological aspect. But this aspect being an introspect (if the term may be excused), it follows that it cannot reach beyond a certain chain of phenomena necessarily limited (at most) to our central nervous system itself. To conclude therefrom the absence of "*consciousness*" (of introspect) for all that is not associated to our individual introspect (to our individual conscience), is simply to enunciate an absurdity.

The said absurdity has been pushed to the utmost limit by the old spiritualistic scholasts who, carrying logic to the extreme, have said: "The world does not exist for me save in the workings of my mind; therefore this latter alone exists, and the outer world, including therein my so-called fellows, does not exist." To such an agreement Molière retorts by means of a cudgel applied to the spiritualist. But the materialists who fancy that they can construct the consciousness (that is to say an aspect, an abstraction) with atoms (another abstraction) simply enunciate another foolishness of the same kind and no less absurd.

I presume that it is absurd to refuse consciousness (introspect) to what appears unconscious to us. In reality, the force of facts obliges us to reason by analogy, that is to say to attribute this introspect, this consciousness, to our fellows: men, women, children, negroes, Veddas, lunatics, idiots even; without which psychology, reduced to each individual ego, would become a myth. But then we cannot refuse it to the Neanderthal man, nor to *Pithecanthropus erectus*, nor to the gorilla, nor to the dog, and then where shall we stop? Can we refuse it to our spinal marrow, if we allow it to the rabbit and to fish?

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[1] I have called neurocyme the molecular dynamic wave which transmits the stimuli in the neurons of the nervous system.

But this is not all. The greatest error is that which perpetually confounds the idea of consciousness, that is to say the abstraction which we draw from the phenomena of our introspection in itself, with the introspected (again excuse the term) cerebral dynamic synthesis. *What is complicated in us are the cerebral forces in play; it is not the consciousness of them, their internal reflex;* in other words, it is the introspected synthesis and not the abstraction of the introspect.[1] To put the matter more clearly, psycho-physiological experiment proves without trouble (Höffding) that what, introspected, appears to us united (as the sensation of red), is composed physiologically of complex dynamisms. The mind is therefore a word of double sense which must represent in reality only the introspected cerebral activity, in the monistic sense of identity. Only the mania of men to be satisfied with words instead of ideas, after their having extracted from psychological phenomena an abstraction devoted to the word "*consciousness*," drives them to give body and feet to this word. Qualifications have been given to the "*consciousness*" to introspection; a mind-force has been made of it, a something which appears at a certain epoch in the animal series (our self-styled contemporary dualistic-materialists like Bethe and others) like the materialised spirits which modern charlatanry evokes to mystify their "adepts," the ghosts and phantoms which in the good old times haunted the towers of ancient castles. To be consistent in his dualisms,

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[1] See Forel, *Der Hypnotismus*, Stuttgart bei F. Enke, 2nd Ed. 1891, and 3rd Ed. 1895, pp. 1-15; then Forel, *Un aperçu de psychologie comparée*, Année psychologique de Binet, 1896, and *Nochmals das Bewusstsein*, Zeitschrift für Hypnotismus, 1894. Without having understood my first point of view, M. Claparède (see below) answers the question, "Are animals conscious?" by the reply, "I do not know, it matters little to me." It is clear that we are not far from agreement. The manner in which we understand the term of consciousness and the psycho-physiological identity makes it absolutely useless to discuss the question of knowing if animals are or are not "conscious." But to say "I do not know," is going too far, unless M. Claparède is willing to know nothing about the *consciousness* of the human beings outside himself. There is here an insensible gradation from knowledge to ignorance by all the degrees of probability. It is enough to study hypnotism to be sure of it.

Descartes decreed that animals were machines, and that the mind of man, posted in the pineal gland, there curbed the body (the brain) by the two little fasciculi of white fibres called in this honour "*habenulæ*"!

What astonishes me is that modern scientific psychology perpetuates this mistake by the term of parallelism, which makes believe that there are two things, and perhaps even a third between the two, where there is in reality only one. The authors who continue to ride on this term of compromise, in wishing to prejudge in favour of a dualistic misunderstanding, constantly forget that introspection only gives us the reflection of a synthesis of forces projected in the cortex of our front brain, whilst they are there reinforced by the concentrated force of the attention (apperception). On its side physiology cannot penetrate into the reciprocal play of the intercerebral neurons, and persists, by confining itself in its methods, to make the legs of frogs dance with electric stimuli, to make gross lesions of the brain, as Goltz has done, or to multiply the number of what it calls "centres" and "reflexes."

So long as physiologists thus limit their field of investigation without taking sufficient account either of anatomy, histology, or human and comparative pathology of the brain, or of the combined experiments with these various disciplines (Methods of Waller and Gudden), or especially of biological and psychological observation, mutual understanding will not be possible. It is enough to reflect an instant on these facts to understand that we are yet a hundred leagues from being able to establish a true "parallelism" between the so-called psychological and physiological phenomena, because between these two kinds which are accessible to our investigations *there are immense accumulators*, inhibitors, and dynamos *of forces* (*cerebral trunk*, *cerebellum*, *cord*, *subconscious cortical activities*) *inaccessible to both methods*.

But these facts are precisely of a nature to strengthen us more and more in the hypothesis of the monistic identity. The present impossibility of bringing back psychology to its physiological "correlatives," as we bring inorganic atoms to their dynamical "correlatives," does not come from a different reality of the two series of phenomena, capable of reaction some on others, but from the difficulty, hitherto unsurmountable, which is opposed to the study of functions (called subconscious) of an immense part of the nerve centres which are inaccessible at the same time to introspection and to the so-called physiological method, to psychology and physiology, which falsifies all our calculations. We here find ourselves in a situation analogous to that of the astronomer whose calculations show a perturbation which proves to him the existence of a star yet unknown. But the astronomer deals with facts more simple, and can discover his star by telescope with the help of his calculations, whilst the functioning of the nerve centres still offers us too much of the unknown to allow us to fix a law like that of Weber-Fechner. This law is not a law. If we leave the hypothesis that the phenomenon of introspection is absolutely general, that it is to all active force as the shadow is to the light, or as the concavity of an ideal mathematical curve is to the convexity of the same curve (Spencer), that, being nothing by itself, it can neither know, nor be complicated, nor have any action whatsoever, we shall understand that what knows or does not know in us is the cerebral activity and not its reflex, the "so-called" consciousness. When it is plastic and complex, when it is endowed with a tendency to combine numerous activities, to compose of it new constellations, sensory or emotional, this activity will constitute the imagination, mother of Genius. When it will tend to assimilate and to reproduce much, it will represent the receptive talent. A strong tendency to actions long prepared by plastic combination will constitute strong wills. The high development of sympathetic emotions and social instincts will furnish the moral sense, etc. Reduced, on the contrary, to its most simple expression, descending by automatism to the reflex, to the amœboid cell, to the atom itself, activity, nervous, protoplasmic, atomic, will not be more than an introspective reflex corresponding to its own complexity, and finally infinitesimal.

I admit that we are much less able to *prove* the existence of this introspective reflex in the cosmic elements of the world than in any complex living organism situated outside of our individual ego. But there is no necessity to give here syllogistic proofs. We must see if the innumerable scientific inductions, which all agree to bring us to the monistic hypothesis, have or have not to be seriously taken into consideration.

And I presume that they are right as long as no one has demonstrated the existence of *a complex mind without a living brain.* In reality, if our introspective phenomena of so-called consciousness are absolutely connected, in what concerns the complexities that they reflect us, with the existence of complicated neurons, it follows that they are the neurons; and their complicated functions, which constitute our mind and not their subjective reflex, that "consciousness," a reflex which is by itself nothing other than the whole of the introspective synthetic aspects of cerebral atomic activities.

And this is why I do not use the term of psycho-physiological parallelism. There is no real parallelism. There is irregular diversity of aspects, because of the great number of unknown quantities interpolated. But at the foundation of everything there is absolute identity of being between matter-force and consciousness in the living brain as in every atom of the universe. This is what must be understood by monism. And what makes us admit its reality is that it takes account of every aspect both mental and material of that nature that has been theoretically and erroneously sundered in two.

Several facts will make the matter better understood. When I look at the blue sky I am conscious of a sensation of blue. This is a phenomenon of introspection. Physiology tells me that the sensation of blue results from a stimulation of the retina by so-called luminous waves of a certain length which are only one form of mechanical vibration, but that the sensation of blue is only produced in me when these waves are reflected by the neurons of a certain portion of the cerebral cortex. But the form in question of the vibration of the said cortical neurons and the sensations of blue cannot exist one without the other. No blue without cortical vibration; no cortical vibration of the said nature without the sensation of blue. The last proposition sometimes appears invalidated as a result of the phenomena of inhibition (but then the cortical vibration is inhibited and therefore does not take place), or by the phenomena of amnesia or hypnotism.[1] But the facts of "double consciousness" have pointed to the mistake, and have proved that we take at every moment phenomena of dissociation or amnesia for cases of unconsciousness. Doubtless the "law" of Fechner does not allow us to measure the psychological by the physiological intensity. But we have seen that this comes from our incapacity to observe the real physiological dynamism which corresponds to the psychological phenomenon. What we measure is always too peripheral. The inhibitions and the dynamogenies (Hemmungen und Bahnungen) of intermediary centres falsify our calculations, and in every way the measure of intercortical and intracortical activities is impossible to us. All these facts tend to confirm that the phenomena of our psychology are only the introspective reflex of attentional cortical physiological phenomena, and are only one and the same thing with them. Hypnotism shows to satiety that this introspective reflex contains a crowd of cerebral phenomena which usually remain unperceived by us, not because they are inherently imperceptible, but because the conscious reflexes of various cerebral activities are divided and cannot be called into play all at once, nor be all recalled in what we call the field of our ordinary consciousness in the state of waking. Hence the fact of subconsciousness or secondary personalities. But these are limited, for our knowledge, to cerebral activities which can, by certain means, be occasionally associated to reflected activities by our ordinary consciousness, that is to say, recalled to our conscious memory. Without any doubt there exists for the lower centres subconsciousnesses or introspective reflexes, of which the contents, for the reasons indicated already regarding the numerous cortical activities, can never *a fortiori* be associated to that of our higher or ordinary consciousness.

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[1] I refer in this regard to the singular case which I observed and which has been described by Max Naef in his doctorate dissertation (Max Naef, *Ein Fall von temporärer, totaler, theilweise-retrograder Amnesie durch Suggestion geheilt*, Zeitschrift für Hypnotismus, Leipzig bei Ambros. Barth, 1898).

A gentleman (hysterical), who had been several months in Australia, there suffered from a slight Dengue fever, which caused in him on May 6th a somnambulistic attack with partial mental dissociation accompanied by sub-consciousness. In this condition he returned, half-dreaming, but nearly recovered, to Europe, abandoning all his engagements, which he had forgotten, and no longer knowing whither he went nor why he was there. He landed at Naples and went to Zurich, where he lived several weeks without suspecting what he had done, without giving any news of himself to his distressed family, who thought him lost. A journal fell into his hands; he there read his story, and concluded therefrom by the name, and by finding his passport in his pocket, that "this must be him." Then, in despair, he came to me and I admitted him to the asylum which I then directed. Up to that moment he had absolutely forgotten eight months of his existence (all his residence in Australia and part of the time before and after). This was in July. By the help of hypnotic suggestion I managed with great trouble at first to make him remember what passed during his absence from Europe. Day by day, in numerous séances, I got him back all his memory up to May 6th; up to that date all his recollections were normal and absolutely logical and exact. But from that it went no further. I then took him in the opposite direction, from leaving Zurich (July), and I managed with great trouble to make the recollections of the somnambulistic state in May and June revive in hypnosis up to May 6th. But these recollections were without logical bonds, dissociated like dreams. These were episodes unconnected and badly interpreted by him. There were therefore two periods in the amnesia: the first, from November to May 6th, during which a normal higher consciousness corresponded to a normal cerebral condition (retrograde amnesia); the second from May 6th to the month of July, where to a dissociated cerebral activity (somnambulistic) had corresponded a subconsciousness related with it. Notwithstanding both had been so well forgotten that from the first time of his residence at the asylum M. X. did not recollect anything by seeing the letters which he had written from Australia, only recognising in them his handwriting. He left cured. I refer to the original for the very curious details.

The psycho-physiological identity is very simply explained if one admits for every nerve activity, and not merely for those which fall ordinarily or accidentally in the domain of our higher consciousness, subconscious introspective reflexes, that is to say, not associated to the said higher consciousness (to reflexes of the apperceptions which constitute its contents).

Every modification of the part of our cortical activity which is to us ordinarily conscious, implies a corresponding modification of our states of consciousness and vice versâ (see the case of amnesia quoted in the footnote above). There can be no doubt but that the maniacal excitement and the melancholic inhibition of persons of unsound mind correspond to pathological conditions of acceleration and retardation of the activity of cortical neurons. During the rest of sleep there is a corresponding dissociation of dreams. To hallucination must correspond a cortico-fugal co-irritation of the neurons which pass from the secondary centre to the cortical centre of the hallucinated sense (thus, for vision, the neurons from the external geniculate body to the cortex of the cuneus), and which normally only conduct cortico-petal stimuli. The study of aphasia and of all that resembles it (group of syndromes of dissymbolics of Kussmaul), in general that of affections of speech, enables us to gain some idea of psycho-physiological identity, just as the study of hypnotism by the help of which we modify at will the reflexes of the consciousness and the functions which represent the ego by the simple introduction into the brain, by means of the channel of the senses, appropriate suggestive representations. Hypnotism is a psycho-physiological game. It is not pure psychology. In reality, one mind can act upon another only by the channel of the senses, which is physiological. It is true that by this channel, by means of words, it awakens representations, emotions, volitions, abstract ideas, etc. But all these psychological phenomena, awakened by associated words, that is to say by the currency of thought, can only be awakened by means of sensory stimuli actual or passed. *Nihil est in intellectu quod non prius fuerit in sensu.*

In a word, we see consciousness always and everywhere simply reflect the cerebral activities. Its content fluctuates and is modified according to the kind, the intensity, the extension, and the duration of the said activities. These activities ceasing, their reflection disappears with them. It is not here a question, therefore, of a parallelism, but of an identity.

How can one, without admitting the subconsciousnesses of the nervous activities which appear to us unconscious, and having regard to the fact that the intensity of a cerebral activity is not in any constant relation with the clearness of the consciousness of which we remember, speak of parallelism, since then one of the parallels (the psychic) would be interrupted at each instant, while the other is not interrupted? The monistic hypothesis, not considering the consciousness as anything, but merely as the introspective aspect of all cosmic activity, an aspect which, in the special case of our psychology, is extended and associated quite naturally with the special extension and association of the attentional concentrations of the cortico-cerebral neurocymic work, the monistic hypothesis, I say, experiences no difficulty in considering psychological phenomena as the introspective syntheses of physiological phenomena. The "consciousness" implies no special, or mysterious, or other force, does not cause us the least difficulty, and upsets in no way the law of the conservation of energy, whilst dualism is even the negation of this law.

The monistic hypothesis allows us further to handle freely comparative psychology while avoiding at the same time Bethe's dualistic anthropomorphism. And this is what interests us here, what we wish to attain.

Parallelism anxiously avoids considering by turns the same fact under its two aspects, physiological and psychological, because it fears, it says, the mistakes which may result therefrom. It wishes to make an absolutely separate study of the two "series." The intention is praiseworthy, we do not doubt. But monism fears on its side that, by separating by words, or even by a whole terminology, Bethe-like, the two aspects of real unities, one may end by falling back heavily into dualism. One fears anthropomorphism too much, and one falls into the opposite extreme. If one wishes to remain consistent, the so-called physiological terminology of Bethe becomes simply impossible. Even when an animal gives undoubted signs of fright, joy, anger, memory, affection, we ought to invent some Greek words coupled to the term of reflex to designate them, for fear of being accused of anthropomorphism. But, then, ought we not to extend these terms to negroes, children, mad people, women, and finally to everything which is not our ego? We prefer freely to grapple with the difficulty by admitting at once that everywhere, at least where there is a central nervous physiology, there must be a corresponding introspection, and to endeavour to condense more and more closely its peculiarities, and by fixing its physiological or biological conditions (which we can observe), to measure and compare by careful experimentation on the habits of the animal. At the same time, reasoning by analogy, we should endeavour to deduce therefrom what this animal psychology might be, in what it differs from and in what it must resemble ours.

Oswald Külpe (*Zeitschrift für Hypnotismus*, Bd. vii. Hefte 1-2, 1898: *Ueber die Beziehungen zwischen körperlichen und seelischen Vorgängen*) puts the dialectic of a past-master of logic at the service of parallelism and also of dualism. He opposes himself to Höffding and others who give to the former a monistic tendency and defines it as prejudging nothing. We have seen that it prejudges too much or too little, according to the way in which one understands it. Külpe cannot admit with Mach and Boltzmann that the idea of cause and effect ought to be replaced by that of the transformation of energy or action and reaction. He points out that if it is possible in mathematics to replace it by the notion of the "Function" which can be applied indifferently to both terms, this is not the case in natural science, where *time* always gives the antecedent independent of the subsequent factor. Very well, but if the law of conservation of energy is true, the subsequent factors may be rediscovered, changed, it is true, but complete, in the antecedent, and the difference of position of the subsequent relative to the antecedent is only a change of form. A second subsequent may in its turn replace the original form in the future. We cannot enter here into dissertations on the theory of knowledge. To the hypothesis of identity can only be opposed that of dualism, that is to say, of a reciprocal action of " the mind " on " the body," unless one denies one of two categories of phenomena, physical (spiritualism) or psychic (materialism), or wishes at least to explain the ones by the others, which leads to an absurdity or to a vicious circle.

Parallelism tries to avoid prejudice towards either dualism or monism and to leave the door open to both. In this sense it gives itself the unassailable air of an indefinite truce. But the danger here consists in taking the truce for something, for a kind of solution allowing the two roads to run without junction. But the facts of both cerebral and biological science agree so well with the monistic hypothesis of identity, and the said hypothesis, provisionally admitted, is so fruitful of inductions which can be further controlled by experiment, that we prefer *to make it the basis of our work until a single irrefutable fact appears which demonstrates to us that it is invalid.* Külpe says that we have no certain means of knowing if the psychic phenomenon is synchronous with the physical phenomenon or if the one precedes the other. But if the one preceded the other (was its " cause " in the common sense of the word), this would have been proved long ago. Being only one and the same reality, there can be no question of one being subsequent to or the cause of the other. To maintain the possibility of dualism, in order to be able to postulate parallelism, Külpe declares that the notion of energy must be demanded as an integral part of the notion of the "mind," without which *reciprocal actions* demand a "diminution" or "increase," and not merely "conservation" of energy. But what, then, is this "energy of the mind," except a play of words, a mind which is rematerialised after having been artificially extracted from natural realities? This smacks terribly of the spiritualists' "materialised spirits," and admits, in my opinion, the justice of Höffding and Mach's conclusions. It is a harking back to the "conscience force" which some authorities, like Bethe and others, would make arise, no one knows whence, in some place in the animal series. To what good are all these dialectical expedients, when the monistic hypothesis gives an account of facts simply and naturally? The mind independent of the law of the conservation of energy (see Wasmann, below Uexküll) is an illusion, but it is less illogical than Külpe's theory.

At the final stage in the endeavour to separate the two series of facts, we find Professor Lipps, at the Psychological Congress at Munich, anxious to separate entirely the disciplines and the men who study them, which I consider wicked. Indeed, the narrow subjectivism of the specialisations applied to two sides of the study of the same facts can only further augment the mistakes already pushed to absurdity. If one has committed an error in wishing to cut the brain somewhere between the Pons Varolii and the Corona radiata, one will commit a double mistake in wishing to separate the *psychology* from the *physiology of the brain* in the same function of the same cerebral neurons.[1]

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[1] To be assured that one does not grossly err, it is good occasionally to examine the arguments that professional psychologists oppose to us when they deign to do us the honour of quoting us. In an article in the *Revue philosophique* (1901), M. Ed. Claparède, Priv. Doc. de Psychologie to the University of Geneva, after having criticised from cover to cover various authors, partly, however, justly, as Loeb, devotes to us the following phrases :—

"M. Forel himself thinks to throw light on the whole subject by adopting an analogous polypsychism (to that of Durand de Gros). But we find ourselves quite naturally exempt from discussing these views, because, contrary to the spirit of parallelism, they are not of a nature to bring us the desired light. Were the

I will point out in ending this chapter, which has already become too long, a work of G. Heymans (*Zur Parallelismusfrage*, Zeitschrift für Psychologie und Physiologie der Sinnesorgane, 1898, Bd. xvii. p. 62), where the author breaks a lance in favour of modern monism and endeavours to make it understood in the language of the psychologist. This work is very clear, and puts a finger on the inconsequences to which dualism leads in regard to an actual knowledge of the brain. M. Heymans, whose article quoted I recommend, speaks of a "*parallelistic monism.*" In the sense in which he understands the latter adjective, I have nothing to object to it, and as far as concerns monism, his opinions seem identical with what I have always held to be its meanings.

polypsychism of MM. Durand de Gros and Forel a hundred times demonstrated, that would not settle an atom the *why* of this double consciousness. It will only drive back to the inferior centres the difficulty before which, in the cerebral cortex, we stood disarmed; it will remain therefore to explain the influence of this 'medullary mind' on the spinal cord, and that is precisely the question. Moreover, this influence admitted, it would be necessary to show (this is what has not been done and for good reason) how the mind knows when it must respond to a certain stimulus in such a way and how it is to set about doing it. The mind is thus invoked as a *Deus ex machina*; that is to say, that science *ignores* what is the reason of our subjective states. It were better to commence by it."

These confusions condemn themselves. M. Claparède has evidently only read two small articles which I published in the *Revue* of Ribot and in the *Annde Psychologique* and has not understood them. In speaking "of the influence of the medullary mind" on the spinal cord, he attributes to us the very dualistic absurdities that we are fighting. We speak neither more nor less of the influence of the medullary mind on the spinal cord than that of the force of an atom on its own matter, because we consider them as two aspects of one and the same energy! It is not "the mind" opposed to the neuron which "knows"; it is the *brain-mind* energy. This is not a *Deus ex machina*, but a *Deus in natura*. It only knows what it can know in the restricted domain of its energies, and only wishes what it can wish for the same reason. And we ourselves, being only a brain-mind, neither presume nor have we ever presumed to explain the metaphysical "why" of our being, a "why" *quite as unfathomable for us under the so-called objective or physical as under the psychological aspect*. This is an old philosophical truth which no longer ought to need repeating. By the help of the hypothesis of monistic identity, once again, we wish in no way to prejudge the metaphysical why; we wish simply to explain to ourselves natural facts observed under their two aspects, physical and introspective. For my opinion on the question of free-will and of what the mind can or cannot know, I refer M. Claparède to my other works published in German on these subjects (*Gehirn und Seele*, *Zurechnungsfähigkeit*, *Hypnotismus*, etc.), but in every case a psychologist ought to see more clearly.

Uexküll. Reply of Wasmann. Bethe: Independent Function of the Nerve Fibrillæ. Loeb

I must beg the reader's pardon for my long excursion into the domain of monism. But I hope that he will have understood the necessity of making clear my standpoint on the fundamental question of all psychology. In refuting the dualisms of Bethe and Wasmann, and in starting from the principle of the psychophysiological identity, we open to psychology the door of vast and fruitful studies, a door which some would close to us.

In the *Biologische Centralblatt*, Bd. xx. No. 15, Aug. 1, 1900 (*Ueber die Stellung der vergl. Physiologie zur Hypothese der Thierseele*), Uexküll lays down punctiliously his extreme (and as he thinks, consistent) views. He has brought there Alb. Bethe himself who, as a converted sinner, acknowledges to not having gone far enough, to having made too many concessions to comparative psychology, and now sides with the opinion of Uexküll. This is perfect and makes our task easier.

The following is pretty nearly the reasoning of Uexküll.

Starting from the peripheral nerve irritation in the animal, and passing by all the nerve centres, one always comes to the muscle. One nowhere finds a "psychology" on his way. The cause of movement can only be, therefore, a movement. For the naturalist, animal psychology consequently does not exist, but merely a nerve physiology. If we could follow in ourselves the molecular nerve movement with a galvanometer, it would be the same for man. But further, at a certain point of our human brain, psychology appears. Between the two there is psychological physiology. This follows the physiological phenomenon as far as the appearance of the psychological phenomenon which was wanting up to that point. But psychical phenomena, suddenly supervening afresh in research, are not come from the physiological phenomena observed up to then, for these latter continue to be produced as heretofore according to fixed laws. This is the cardinal point. Indeed: If a movement can only produce a movement, and if the chain of causes and effects is complete up to the execution of the last movement produced, the first movement cannot produce apart from that a "psychic quality."

Between the movements of the material points in space and my sensation there is no relation of cause (no more indeed than between light and shade, or between the mathematical line and the series of points which constitute it—Forel). With whoever has not understood this fundamental axiom of psychological physiology, all discussion is useless. That is what Uexküll says.

As a new discovery, Uexküll teaches us that one cannot make a colour-blind person grasp the idea of colour, which is wanting in him, be he never so profound a psycho-physiologist! What is so amusing is that Uexküll, despite his absolutistic consistence, only attacks animal psychology, but not that of other men. Wishing to be absolutely consistent, he commits a gross inconsistency. For him only one psychology must exist, that of J. V. Uexküll.[1]

We cannot, he says, know if an ant recognises blue, red, salt *like us*. Therefore we cannot attribute memory, sensation, psychic qualities to it. We will not return to the falsity of this reasoning, which we have already sufficiently demonstrated in dealing with Bethe. Uexküll declines, therefore, either to affirm or deny sensation in the insect, this problem being in his opinion quite out of our horizon (let us say of the horizon of a specialist in physiology who has eyes closed for all that is not akin to his methods).

Instead of saying: "The recollection of the smell of the nest at this moment arrested the attention of the ant," one can say accordiug to Uexküll:

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[1] Uexküll does little else but make negative and dogmatic criticism with an arrogance, very amusing nevertheless, which has been very well characterised by Willibald Nagel (Zeitschrift für Psychologie der Sinnesorgane, 1896), to the works of whom I hope to be able to return elsewhere. Nagel lays his finger on the exaggerations and inconsistencies of Uexküll, the method by which he distorts the thought and the terms of those whom he criticises, finally the absurdities to which his extreme point of view leads. Uexküll, absolute partisan of the dogma of the absolute special energy of each sense, criticises, for example, Nagel violently because the latter has very well shown the points where the "dogma" has its limits. Uexküll completely forgets that the phyletism of the special energies must make them derived little by little from energies not yet specified, and that by the help of adequate stimulating agents to which they have been little by little adapted.

"The stimulus produced by the substance of the nest which had remained latent in the central organ, became again active at that moment."

From this simple case Uexküll almost extricates himself, although very clumsily, with his physiological language, but I beg the reader to make the attempt himself to describe animal biological observations in similar physiological jargon to see where he will end, even if he interpolates into it ten or twelve letters designating the "unknown forces" of the Bethe genus! For my part I give it up.

Finally Uexküll ends by summing up almost as follows: The hypothesis of animal psychology in comparative physiology leads to nothing positive, but causes a terrible confusion. The results are anything but science. We have put all this old rubbish into the basket, without any more ado, like alchemy and astrology. Experimental science is occupied only with what can be weighed and measured. Beer, Bethe, and I place ourselves consequently at this point of view, and invite all our colleagues quietly and energetically to show the door to all speculation on the unknowable!

Brrr! That settles our business! Therefore, according to Uexküll, we only make divagations on the unknowable. In his reply to Uexküll, Wasmann at first declares the complete conversion of Bethe to the ideas of Uexküll. Then he throws himself into dualism and clearly enunciates that psychological phenomena cannot be submitted to the law of the conservation of energy (see above, Külpe, who proves us the contrary). It wants little for Wasmann and Uexküll to agree on metaphysical dualism. What seems to make them right is the false monism badly understood of Haeckel or Flechsig. These authors believe they have found "a special organ for consciousness," for subjectivism, which they confuse with the cerebral work of thought.[1] We refer to what we have said on this subject.

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[1] As regards Haeckel's monism, I cannot find that he has ever attempted to suggest a "special organ for thought"; he persistently asseverates that what we call "mind" is the result of the cerebral activities. True, he calls the cells of the cerebral cortex the "*phronema*," but this is merely a term specially distinguishing the cells which are concerned with thought. I confess that I cannot distinguish the monism of Haeckel from that of Forel.—Trans.

Moreover, Wasmann (Biolog. Centralblatt, Bd. xxi. No. 1, Jan. 1, 1901: *Nervenphysiologie und Thierpsychologie*) gives an excellent reply to Uexküll, which I recommend to every reader desirous of instructing himself, despite the dualism which is hidden under the terms of reciprocal action (*Wechselwirkung*) and of cause and effect applied to psycho-physiological phenomena, a mistake which we have eliminated above.

As regards cause and effect, let us again point out a great confusion. It goes without saying that one can (Wasmann rightly insists thereon) consider the stimulating agent of a sensory nerve (a wasp sting, for instance) as cause of the sensation of pain which follows it. In denying this, Uexküll has made an absurd statement which Wasmann has taken up. But this is not what the theory of identity says. This latter compares a sensation of blue, for example, to later synchronous cortical neurochymic waves, without which the sensation does not take place, and which cannot be produced without sensation. Whilst in the case of the sting we shall compare a phenomenon of the extremity of a cutaneous nerve to another phenomenon subsequent and cortical, and must conclude therefrom action and reaction or cause and effect (relation between two subsequent realities in sequence), in the case of the sensation of blue and its "cortical physiological correlative" there is synchronism and identity of reality. For the sting similarly exist "synchronous cortical neurochymic waves" identical to the sensation of pain. Concerning "sensations" the peripheral nerve and the subcortical centres can and must have, they are subconscious and we do not know of them.

Doubtless, if we never get beyond physiological methods, we shall find nothing but movement, and for my part (Uexküll will find therein a little excusable impoliteness on the part of those whom he handles as "astrologers with their ancient rubbish"), if I am limited to study the motor reactions of M. Uexküll, from the entry of his photo-receptions and to the exit of his movements graphically fixed by the printing-office, I shall also be obliged to deny that he may have a psychology, and I shall even find his physiological reactions too simple to be exact or worth consideration: I hope he will excuse it.

But let us finish with this ridiculous jargon which involuntarily provokes irony in a very serious subject. Uexküll forgets simply, as Wasmann well pointed out to him, that we have other scientific methods besides that of physiology. I have shown above what enormous exaggeration it is to call physiology an exact science.

Psychological observation, induction, and well-based analogies lose nothing of their scientific rights because of the various caprices of authors whose presumption is only equalled by the weakness of their logic, and, as we have seen, by the superficiality of their observations.

The first reasoning of Uexküll would be just if we might presume that the molecular movements of the central nervous system *produced, apart from the motor effects, psychical qualities.* But it is precisely this false idea which the theory of psychological identity upheld by us combats, and, in attacking us, Uexküll confirms us. One and the same reality can neither produce itself nor be itself its own cause, *quod erat demonstrandum.* Then why refuse to the introspective or psychological method the study of this reality? That has nothing to do with the physiologist, Uexküll will reply. And in that he gives proof of that narrow spirit of the specialist which insists upon knowing only his side of the question. When Waller and von Gudden instituted their admirable and fruitful anatomo-physiological method of studying the nerve centres by means of secondary degenerations and atrophies supervening on lesions, operative and other, of certain centres or peripheral nerve organs, their fundamental results were long ignored by physiologists who said, "This is not physiology," and by anatomists who said, "This is not anatomy!" In thus doing, they acted like Uexküll, Bethe, etc., not from science, but from the narrowness of the specialist, often more dangerous than alchemy.

In his artlessness Uexküll, who notwithstanding works and observes Nature only with his own psychology and his own subjectivism, does not perceive that his "axiom" makes him deny all human psychology other than his own, and all biology "which is not studied with the anatomo-physiological method," in a word that it conducts him to the most complete absurdity. We are compelled to recall to him that the deductive method is *exact* only in pure mathematics, for the reasons pointed out above. But the true scientific or inductive method excludes exclusivism and unilaterality. It demands that *all* the methods accessible be used to reach little by little, by the comparison of their results, to the relative truth, which alone we can know. Therefore, for the human and animal brain as well as for its functions, it demands that we shall use anatomical, physiological, biological, and *psychological* methods, and that we shall compare their results by the aid of inductions, homologies, and analogies while we accumulate facts. Doubtless applied mathematics will be used to physical and chemical problems wherever it will be feasible. But it is childish to think to confine our reasoning within mathematical limits.

Psychology is a science of observation, as so many others, and the scientific method requires here so much the more the employment of other, not mathematical, methods for investigation, since we have no mathematical base to calculate cerebral biology, which makes absolutely ridiculous and absurd the pretences and exigencies of Uexküll. With his system one comes to be satisfied with words, that is all; the endeavours of Bethe, criticised above, are amply loaded to demonstrate it.

Finally let us reply to an objection which has been made to us more than once, and according to which the "consciousness" would be a psychical *quality* which has achieved development, like any other quality, at a certain moment in the phyletic series, or which "appeared" at a certain moment of ontogenesis. The idea (Begriff) of psychological quality is a purely subjective one. We do not know objective qualities. The so-called objective comparison and verification of the impressions of our various senses, by the aid of the others, concerns only quantities. As far as qualitative difference is concerned, we rely directly or indirectly on the sense, or on memory of our sensations. In combining the latter we draw therefrom, by abstraction, abstract qualities (beauty, ugliness). The notion of qualitative difference of sensations is, with that of the sensation itself, the fundamental and elementary idea of psychology. If, therefore, we call subjectivism, introspection, or consciousness the general abstract idea which comprehends all special ideas of qualitative or psychological aspects (not the cerebral dynamisms which they reflect!), it follows, therefore, that we cannot make it derived from a special case, nor compare it to a special quality, any more than we can say: "force" or "matter" has appeared at a certain moment and on a certain point in the universe, or is "derived" from this or that.

The common retort is, that since we know subjectivism only from ourselves, we cannot externalise nor contribute it to what is outside the introspective field of our higher consciousness in the state of waking. We have seen that in reality, save for the facts brought to light by hypnotism and the said cases of double consciousness, we can only reason thereon by analogy, but we have given at the same time reasons which speak for the monistic hypothesis and we do not return to them. We declare only that the theory of psycho-physiological identity which, we have seen, avoids for us a tissue of contradictions and wordy disputes, makes very probable the existence of a subjectivism (that is to say of a subjective or introspective aspect), not only in the beings which resemble us where it cannot be put in doubt, but in every reality, living or other, outside us. Only this hypothesis loses its scientific importance, as we plainly recognise, according as we are separated more from complex nerve centres resembling our own, and ends by becoming identical with the monistic metaphysics (Spinozist monism), where we must not follow it so long as we confine ourselves to the region of science. We are nevertheless obliged (by logic) to point out this metaphysical hypothesis, because its possibility (or, as I think, probability) avoids for us the contradictions into which the world would like to place us by the help of other metaphysical dogmas which authority always seeks to impose on us, either directly or *sub rosa*.

In ending this chapter, let us thank MM. Bethe, Uexküll, and Beer for their exclusivist campaign. It has had the great advantage of making us state precisely terms and methods, in fortifying the *raison d'être* of the eclecticism necessary to all biology or comparative psychology.

Before taking leave of Bethe and Uexküll, as well as of their hypotheses which leave everything open, may I say two words on an experiment of Bethe (Das centr. Nervensyst. von *Carcinus maenas*, Archiv f. micr. Anat., 1897, p. 629). Bethe says that he has succeeded in separating the antennary nerve of *Carcinus mænas* from *all* its central cells, and to have obtained, in spite of this, reflex movements of the antenna. He concludes therefrom that the neuropilemma (the fibrillæ) can function without the ganglion cell of the neuron to which it belongs. The facts would be indeed very decisive if it was proved. Bethe agrees that the operation is extremely difficult, and has only succeeded with him twice, but, if he is to be believed, his result would be very positive. I confess that the control of Bethe's experiments on bees and ants, as much by von Buttel Reepen as by myself, has taken from me the confidence which I had at the beginning, if not in the judgment, at least in the exactitude of this author. I should have, therefore, good reasons for doubting as to the totality of the extirpation by Bethe under such conditions.

But even if the observation of Bethe is exact, and if his extirpation of the cells has been complete, it in no way proves what the author thinks he has proved, that is to say, *a normal functioning of the neurons of which the ganglion cell has been removed.* Indeed, even one antenna or one foot separated from the body in certain arachnids and insects, continues to make spontaneously the movements of flexion and extension which Bethe has observed; it is an old story well known to every entomologist. It is sometimes so also when its sensory terminations are stimulated. But the sensory terminations of the antennæ (terminal antennary ganglion) are cellular and not fibrillary like those of the skin of vertebrates. Bethe has therefore suppressed only the cells of centrifugal neurons, but not those of the centripetal neurons which still-lived beneath the cuticle of the antenna of his *Carcinus*! Further, Arloing, Tripier, and others have proved in vertebrates the existence of a recurrent sensibility by means of sensitive fibres existing in motor nerves. Who has proved to Bethe that the peripheral cells of the antenna of his *Carcinus*, isolated from the cerebral centres, did not transmit several recurrent fibrillary ramifications to the motor nerve of the antenna? All is thus explained quite simply by intra-antennary reflexes, independent of the brain. In any case Bethe has not in the least excluded the ganglion cell from the reflexes which he has obtained, as he imagines he did; only these are peripheral ganglion cells and not cerebral cells which may be left in continuity with a part of the fibres separated from the brain.

Finally, the movements of simple flexion and extension of the antenna observed by Bethe following an irritation of the antenna separated from the brain are not necessarily reflex movements. Indeed, when one isolates the muscles of a frog's foot with their motor nerve, one obtains, as everyone knows, a muscular contraction by irritating the cut surface of the peripheral trunk of the nerve supplying the muscle, even when the said trunk is separated from its ganglion cells. So long as the nerve is not yet degenerated (secondary degeneration) this reaction is possible and produces a flexion, if the bones of the foot are still attached to the muscles. It is not a question here of reflex function, but of a replacement of similar action by direct chemical or physical stimulation of a trunk of a neuron. Bethe does not appear to me to have excluded this possibility in his experiments, which, for the various reasons indicated, prove, in my opinion, nothing. Let us further recall the well-known tenacity of local life in the stumps of articulated animals, and the only astonishing thing in the matter is the importance attached to his result by Bethe. However, the irritability of the antenna does not last very long, which appears to show that the sectioned nerve is not slow to degenerate, probably with its intra-antennary ganglion.

I do not speak of Bethe's other physiological experiments on the nervous system, because that digresses from our subject and because they had been already made in great part by Yersin (*l.c.*), nearly fifty years ago, on the cricket. I am only astonished to see the discovery of the fibrillæ attributed by him to Apathy, when Leydig, Kupper, Solbrig and so many others have described and figured them already so many years ago. See, for instance, the work of Solbrig (*Ueber die feinere Structur der Nervenelemente bei den Gasteropoden*, 1872). Apathy has simply followed them further.

To be complete we must further analyse the works of Loeb (*Einleitung der vergleichenden Gehirnphysiologie*, Leipzig, 1899). Loeb has similar ideas to those of Bethe, etc. He thinks he can reduce instincts to the mechanical effects of physical and chemical forces (light, etc.). He has his "word," like the others;

for him it is a "tropism" (geotropism, heliotropism, etc.), corresponding more or less to the "unknown forces" of Bethe. And like Bethe it gives rise to the "consciousness," the "psychism" in the higher animals. But a similar analysis will lead us into mere idle repetition. What I have replied to Bethe, and what has been said in the fourth and fifth parts of the present work, is applied also to Loeb and his badly matured hypothesis. He wants to prove the mechanical laws of life, even when the base is lacking, and cuts in two the activity of the nerve centres, where no breach exists. It is rather we who should have the right to employ the haughty terms of Uexküll, and say that it is time to put on the scrap-heap this *salmagundi* of unproved vital mechanism and superstitious psycho-physiological dualism. There is more of alchemy in it than in simple and modest biological observation, even with its anthropomorphic errors.

Netter, Ziegler

A. NETTER.—Albr. Netter, *Examen des mœurs des Abeilles au double point de vue des mathématiques et de la psychologie expérimentales*; Comptes rendus de l'Académie des sciènces, 10 Dec. 1900.

M. le Dr. Netter, a Cartesian to his finger-tips, had already published a most interesting book entitled *L'Homme et l'Animal* in opposition to the experimental method (Paris, E. Dentu, 1883). In this book he uses all his dialectic to prove that animals have no soul nor intelligence; that they are merely machines. It is a very *tour de force*, akin to sophism, and endeavours to show that the individual experiments of which I have given proofs in my *Fourmis de la Suisse* are the effect of a pure mechanism. He says therein the same of dogs, in short, of every animal. The comparison of his book with the present work is very instructive; it enables everyone to follow step by step the false judgments of Cartesianism, of which the apparent reason is especially that anthropomorphism which was attributed then to the as yet very badly understood animal intelligence. For the Cartesian there is nothing but extremes. He passes from a machine (automatic instinct) to the human mind, without understanding the intermediate stages: and makes of these an antithesis.

In his later years M. le Dr. Netter returns to the charge in regard to bees. If I quote, it is *pro memoria*, for his article refutes itself. It is enough to compare it with our résumé of von Buttel Reepen to see the inanity of Netter's reasonings. Netter thinks he sees in the geometric form of the alveoli of the honeycomb an echo of the mosaic vision of the faceted eye which would furnish the plan of it. Others have seen in it the effect of simple mechanical pressure. O these mechanists! If Netter was right, why should other insects, whose facettes are equally hexagonal, construct rounded, irregular, or tubular cells? And if the pressure can explain the hexagonal form of the honeycomb cells, it cannot also explain the similar hexagonal forms of the paper combs which wasps and hornets construct.

We have refuted in every aspect the so-called proofs of Cartesianism brought by Netter, and we do not fear to recommend to people who wish to be instructed the reading of his dialectic, persuaded that the comparison will bring them to acknowledge us to be right, and to understand step by step the errors whither the syllogistic of the Cartesians leads.

In this regard I allow myself to predict that on the day when we shall have the key to the mechanism of protoplasmic life, of reflexes, and of instinct, we shall also be given thereby that of the plastic activity of the human mind.

H. E. ZIEGLER.—*Ueber den Begriff des Instinctes*; Vortrag von Prof. H. E. Ziegler, Verh. deutsch. zool. Ges., 1892, Freiburg in Breisgau.

Theoretisches zur Thierpsychologie und vergleichenden Neurophysiologie; Biolog. Centralblatt, Jan. 1900, derselbe.

In the first of these two works, Ziegler allies himself with the opinion of Weismann against Darwin. He rightly denies that instinct can proceed from inherited habits, and considers it derived from the conjunction of germs and of selection, like morphological structures. He quotes a discourse of Theodore Meynert (the brain anatomist) delivered at the meeting of German Naturalists at Wiesbaden in 1887. Meynert points out with great justice that, if habits or secondary automatisms are transformed into instincts, these latter must constitute the most elevated and most complicated phase of the human mind of which the individual thought would become useless. But it is the contrary which takes place: the great brain of man, an organ of individual and intelligent associations, holds scarcely any inherited instincts.

Ziegler defines instinct nearly as we do as a complicated and hereditary reflex. We simply add that, in complicating itself with successive co-ordinated acts and tending to an end, instinct departs from the definition of the simple reflex. It is a complicated automatism, composed of successive acts bound by sensorial impressions and plastic intercalations. It is even an hereditary series of automatism, each composed of various reflexes combined and co-ordinated to an object.

I have said several times that the plastic or adaptative reaction is primary and instinct secondary. The reflection of Meynert enunciated above may at first sight appear to contradict me.

This is nevertheless not the case at all. I consider, even as Weismann, instinct as being unable to proceed directly from inherited habits, and the reflection of Meynert strongly supports this point of view. But I consider at the same time the automatism of all nervous activity, whether by selective heredity or by individual habit, as a secondary phenomenon, derived from primitively plastic activities. For individual habit, the fact is patent. Everyone can see it in himself, in other men, and even in animals. We have seen the insects even (bees, ants) giving proofs of it.

For inherited instinct it is more difficult to prove. Nevertheless we observe that instincts are more or less fixed, more or less invariable. But it cannot be doubtful that the most fixed instincts, the most invariable, are the oldest. I will quote, for example, the fixed and fatal slave-making instinct of *Polyergus rufescens*, compared to the as yet non-fatal slave-making instinct, subject to exceptions, rare, it is true, of *Formica sanguinea*. Now, the study of ants clearly proves that the instinct of *Formica sanguinea* is the more recent. But further. The other species of *Formica*, not usually slave-making, which exceptionally make slaves (*Formica rufa*, *truncicola*, *exsecta*, *exsectoides*), reveal clearly enough the plastic origin of the slave-making instinct of the *Formica sanguinea*, their congener. By selection, a disposition yet little marked to certain plastic adaptations is developed more and more in numerous generations, and has ended by becoming more and more instinctive.

The most primitive form of motor reaction of life, the contractility or irritability of the cell protoplasm, is neither reflex nor plastic. It is as yet undifferentiated. But the beginning of all motility can only be plastic at its outset, for it cannot as yet be automatised or fixed, either for the individual or for the species, either by habit or by heredity. Here I am opposed by Ziegler. This does not at all hinder the plastic activity from taking an enormous development in the human brain, thanks to the immense number of its elements not immobilised by reflexes and automatisms. I believe, for my part, that automatic activity specialised itself for its own convenience in the matter of reflexes and simple instincts, in those centres which are closely connected to the neurons of the organs of the senses and of the muscles, whilst centres more specially endowed with adaptative and combinative plastic activity superposed themselves by forming neurons which only receive indirectly sensorial stimuli and convey only indirectly their stimuli to muscles. These latter maintain nevertheless the faculty of automatising their own activities by repetition (habits), and inherit at least tendencies by conjunction and selection. The great independent cerebral hemispheres of worker ants compared with the rudimentary hemispheres of male ants confirm these views in a striking manner.

Ziegler rightly refuses to allow the notion of conscience-force to intervene in instinct, and generally in animal psychology. I shall not return to this matter.

In the second work quoted, Ziegler gives an account of the opinions of Bethe, Beer, Uexküll, Apathy, etc. In my opinion he gives too much credit to the first three authors, to the criticism of whom I shall not return. The histological works of Apathy need not concern us here.

Ziegler takes the opportunity of this revision to introduce some new terms which appear to me superfluous.

Instead of *heredity* and *hereditary* he says *cleronomy* and *cleronomic*, applying these terms to reflexes and instinct. What is the advantage of this Greek word, when a word clear and distinct, known to all, expresses the same idea?

Anticlisis or *faculty of modification*, is the word that Bethe, Beer, and Uexküll use for what I have called *plastic activity* or *plasticity*. Here again I do not see the advantage of changing the name.

What the individual acquires in its individual life, Ziegler calls *embiontic*. I prefer the old terms *individual adaptation*, *acquired by the action of the surroundings*, *education*, *etc.* It appears to me as simple and as clear to speak of inherited and acquired characters or factors as of cleronomic and embiontic characters or factors.

I have designated (*Gehirn und Seele*, 1894) the nerve wave of molecular stimulation by the term *neurochyme*. Ziegler thinks he must substitute for it that of *neurocinesis*. Beyond the fact that it is longer, I do not see the advantage of this change. Putting aside the law of priority, I think that the multiplication of terms to describe the same thing does not advance our knowledge.

Ziegler supports the opinion of Wernike, who distinguishes between the *memory* (preservation of images) and the *Merkfähigkeit*. For my part I do not understand the difference that Wernike and Ziegler make between their *Merkfähigkeit* and the *attention*. The attentional states are those which are fixed in the first place by the memory. This is not new.[1]

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[1] At the moment when this work left the press I received a work by D. G. Alexander (*Zur Anatomie des Ganglion vestibulare der Säugethiere*; Sitzber. d. K. Acad. d. Wiss. Wien, Math. naturw. Kl., Bd. cviii. Abth. 3, Nov. 1899). The author studies the ganglion enlargements of the nerve of the vestibule enclosed in the petrous bone, and attributes to them *all* the neurons of the said nerve. I cannot examine the fact. If it is correct, it requires the remaking of the experiment of atrophy (partial, it is true) which we have verified of the cells of the nucleus of Bechterew at the base of the cerebellum. In any case it excludes the comparison which we have made between the nerve of the vestibule and the motor nerves.

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